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A STUDY IN PHYSIOGRAPHIC ECOLOGY IN NORTHERN FLORIDA

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(WITH TEN FIGURES)

Introduction

Ecological investigations of the coastal plain of southeastern United States, with few exceptions, have not been undertaken from the standpoint of the relation of physiography to the successional history of the plant associations, nor has the classification of this region been satisfactorily established in comparison with other forest formations of the United States. SCHIMPER (11) mapped this portion of the coastal plain (with the exception of southern Florida) as temperate rain forest. SARGENT (10) classified it as the southern maritime pine belt. The first classification is obviously inconsistent, and the second is open to question if by pine forest is meant a climax formation.

Except for HARSHBERGER's detailed treatment of the coastal plain in his *Phytogeographic survey of North America*, studies of this particular region have been scattered, and usually of exceptional localities. On the Gulf Coast, HILGARD in soil surveys in Mississippi and Louisiana paid special attention to plants as soil indicators, outlining associations on this basis. Studies of island plant life in the Mississippi River sound and delta were made by LLOYD and TRACY (8); while MOHR in his *Plant life of Alabama* grouped

various plant associations belonging to the different geological divisions of the coastal region of that state, comparing the flora in its relationships with adjoining regions and with the West Indies and Mexico. More recently, HARPER has contributed numerous publications containing ecological data, as the result of extensive observations and explorations in various parts of the coastal plain, his most complete works being a phytogeographic study of the Altamaha grit formation of Georgia (**5**), and publications in the reports of the State Geological Survey of Florida (**6**, **7**).

The area described in this study is included mainly in Leon County, Florida. This county is situated half-way between the east and west boundaries of the northern part of the state, bordering the Georgia line and distant about 20 miles from the Gulf of Mexico. The area is approximately 675 square miles, and as a whole is located immediately west of the 84th meridian and between 30 and 31° north latitude.

The topography is diversified, and a soil survey (**14**) of this county locates and describes 12 soil types (including meadow and swamp), of which the most extensive are those also common to the coastal plain from Virginia south to Florida and west to Texas.

This section of Florida has had a varied history, dating back to early Indian tribes and the first Spanish explorers. According to narratives of DE SOTO'S followers, the fame of this country as the "land of plenty" extended to eastern and central Florida, and made it a desirable place to seek for possession and settlement. During the several hundred years of history chronicling invasions and resettlement, therefore, successive clearings of the forest, from the more fertile soils at least, must have been made. About the time of the establishment of the capital at Tallahassee (1823) near the center of the county, WILLIAMS (**15**) described "abundant groves of oak, hickory, beech, and magnolia crowning the hills and covering their slopes." Such early pictures are of interest now in considering the upland forests.

Physical features

CLIMATE.—Weather records have been kept at Tallahassee since 1885 (**3**). The mean summer temperature averages 79°.7, autumn

68°, winter 53°, and spring 67°.6 F., indicating a moderate and equable yearly temperature. There are records of severity, however, the lowest temperature for the state being recorded from Leon County, −2° F. on February 13, 1899. Frost may be expected from November 1 until April 1, the frost record for 18 years giving the date of the first killing frost in autumn as November 4, the last killing frost in spring as April 6, the average date of the first killing frost in autumn as December 5, and the average date of the last killing frost in spring as March 3.

The mean annual precipitation for the Tallahassee station (3) is 57.12 inches, and there are 2 marked periods of rainfall; one (the lesser) in winter culminating in March, and the other (more excessive) culminating in July. This summer rainfall averages 26.8 inches, and the winter rainfall 17.9 inches, the summer rains occurring almost daily as afternoon thunderstorms, while the winter rains are more evenly distributed between day and night. The year is divided thus into wet and dry seasons, more or less marked, April and November being the driest months.

There are no reliable records for relative humidity, although for northern Florida the percentage of relative humidity is highest in September and lowest in April.

These climatic effects combined tend to make spring (April period) the hardest season for plants, so far as the moisture relations are concerned.

PHYSIOGRAPHY.—Limestones of the Oligocene period are considered now to be the oldest rocks of Florida and to form the rock basis for most of the state (9). These limestones also are the surface rock over much of northern Florida, and indicate the earliest and most persistent land surface during subsequent geological history. The presence so near the surface of readily soluble and easily disintegrated rock has doubtless had important influence upon the present topography and drainage, as well as upon the character of some of the soil.

Crossing the country from north to south, the most striking topographical feature is the division of the surface into 2 distinct parts, a highland and a lowland. By this division about two-thirds of the surface is included in the highland, which is a portion of the

narrow upland extending along the northern edge of Florida and into Georgia, and which, on its sea-facing side, often drops abruptly to the more recent coastal strip.

The general elevation of the upland is betweeen 100 and 200 ft. above sea level. The surface is gently rolling with series of broadly rounded or flat topped hills, in general extending east and west, and alternating with open, troughlike valleys. Many of the valley streams are mere swampy or boggy tracts, or they may pursue sluggish courses which end blindly, spreading out on the surface of the ground at the lowest part and soaking gradually into the soil. Others end in ponds which occupy basin-like depressions, or may drain into the larger lakes and sinkholes. In this hill region the sinkhole origin of many large lakes as well as small ponds, and the sinkhole formation along the line of some of the valleys at present, suggest that the depressions of this upland division may be due in large part to subterranean erosion. At any rate, no considerable part of the drainage is now carried off on the surface.

Southward from the edge of the highland there is a gradual slope to the Gulf, the surface being varied only by low swells of sandy soil. The St. Mark's River cuts across these sands in the southeastern corner of the county, part of its present course being due to underground solution. The Wakulla River, having its origin in the flatwoods, flows across the southern part of the county as a typical pre-erosion stream, but is soon lost underground, to emerge at length in Wakulla Spring, one of the finest large springs in the state. Some of the small lakes are quite deep and constant, while the majority are mere pine barren ponds, partially or entirely dried out at times. Other depressions are swampy tracts known variously as "bays," "galls," and "sloughs."

Soils.—As throughout the coastal plain, the soils are chiefly types of sandy series, the Soil Survey (**14**) stating that only about one-half square mile of soil as heavy as loam or clay would be found in the land surface of the county. The hills are covered by soils described as derived from the Lafayette formation, while the valleys and less elevated portions are covered with Columbia sands deposited during a late period of submergence.

Of the Lafayette derivation, the Orangeburg fine sandy loam and the Norfolk fine sandy loam are the most extensive, and represent 2 types found only within the coastal plain of southeastern United States (1). The former is distributed chiefly in 2 belts across the Gulf Coast states and also west of the Mississippi River, constituting the higher lands. The Norfolk fine sandy loam extends from Virginia to northern Florida and west to Texas. In topography it is similar to the Orangeburg, and together these 2 soils are considered the most important for general agriculture, forming the greater part of the so-called "clay hammock lands" (13), characterized by a telling percentage of clay in their subsoils and esteemed for their fertility. The subsoil of the Orangeburg gives the designation of "red hills" so commonly used in descriptions of southern Georgia and of northern Florida, for the freshly cut or eroded subsoil is a bright red sandy clay. The subsoil of the Norfolk is a yellow sandy clay or clay loam.

Of the sedimentary deposits, the Norfolk sand covers the largest area, being the most widely distributed soil of the coastal plain from New Jersey southward (1). It is characterized by low elevation and generally level surface from the immediate shore line inland.

Corresponding, then, with the 2 general topographic divisions there are 2 general soil divisions, that of the more elevated regions having clayey subsoil, while the rest is nearly pure sand.

Vegetation in relation to physiography

UPLANDS

Clay hammock lands

In the study of the upland on these soils, there are few evidences of primeval forests, but it is easy to follow recent reforestation and thus to gain an idea of the succession under present conditions.

The methods of agriculture as long practiced in these regions soon exhausted the soil and led to clearing of fresh tracts. The use of these for a few years and their abandonment and return to forest afford object lessons of all stages of second growth. Also on

some agriculturally less desirable lands it is possible to see a forest recently undisturbed; likewise on some of the old and extensive estates groves have been preserved and illustrate what the forests may have been before the civil war. Clearing and exhaustive cotton growing soon reduce the humus and bring about soil vitiation, which exposure intensifies, resulting in a more xerophytic state.

The exposed Orangeburg soil readily washes, and plants can get a hold on the steep bare slopes with difficulty. Soil lichens and mosses, however, soon form a gray-green coating, especially if partially shaded. Species of *Cladonia* and *Baeomyces* are among these earth lichens.

Fields relapsing from tillage soon grow a mixture of ruderals and native plants. *Cenchrus carolinianus* Walt., *C. tribuloides* L., *Erianthus divaricatus* Hitch., *E. brevibarbis* Michx., *Andropogon virginicus* L., *A. Elliottii* Chapm., *A. scoparius* Michx., *Gerardia purpurea* L., *G. fasciculata* Ell., *G. tenuifolia* Vahl., *Aplopappus divaricatus* Gray, and *Eupatorium capillifolium* Small, with prostrate species of *Rubus* (*R. trivialis* Michx. and *R. cuneifolius* Pursh) are common plants soon covering the old fields, which in a short time are dotted with the seedlings of pioneer pines. Of these pines, *P. echinata* Mill. (short-leaved yellow pine) is by far the most abundant, although other species occur, as *P. Taeda* L. (loblolly or old-field pine), *P. caribaea* Morelet (Cuban or slash pine), and occasionally *P. clausa* Sarg. (sand or spruce pine), and *P. palustris* Mill. (long-leaved yellow pine). *Quercus virginiana* Mill. (live oak) is a broad-leaved evergreen pioneer, and *Diospyros virginiana* L. (persimmon) and *Liquidambar Styraciflua* L. (sweet gum) are deciduous trees soon growing with the dominant pines. *Sassafras variifolium* Ktze. and *Prunus angustifolia* Marsh. are thicket formers. *Pteris aquilina* L. is an abundant fern characteristic of these xerophytic pioneer stages of the old fields.

The pines which spring up in such numbers, if not disturbed, grow rapidly, and on the whole uniformly, and comparatively soon form a forest of trees of similar height and diameter. Where burning or pasturing does not interefere, a dense shrubbery quickly develops, including a variety of seedling trees and shrubs. Of these

developing trees, oaks are most numerous, *Q. falcata* Michx. (Spanish or red oak) and *Q. stellata* Wang (post oak) being the principal pioneers. *Q. virginiana* Mill. persists, being a tree of almost every habitat, from hydro-mesophytic to xerophytic. When forming groves of large, wide spreading trees, draped with *Tillandsia usneoides* L. (Spanish moss) and supporting on the trunks and

FIG. 1.—*Quercus virginiana* on hammock soil

branches a growth of *Polypodium polypodioides* Hitch., this live oak is the typical tree of the mesophytic "hammock," a term used in these regions of the south to designate lands supporting a forest growth of deciduous and broad-leaved evergreen species, correlated with a rich and fertile soil (fig. 1). The evergreen *Ilex opaca* Ait. grows well in the shade of the pines; and *Cornus florida* L. develops under taller trees, sometimes forming an under forest, with some of the trunks 12–18 inches in diameter at 2 ft. from the ground, the widely spreading tops meeting overhead, while above them rise the pines. *Pyrus angustifolia* Ait. (wild

crab) is a small tree characteristic of the pine wood borders and more open parts.

Mingled with the oaks are hickories, *Carya alba* K. Koch being the prevalent species, and a characteristic member of the developing oak forest. The mixed assemblage of small trees and taller shrubs accompanying the oaks and hickories include *Ilex vomitoria* Ait. (an evergreen), several species of *Crataegus* (especially *C. consanguinea* Beadl., *C. robur* Beadl., *C. panda* Beadl.), *Rhus copallina* L., *Callicarpa americana* L., and *Vaccinium arboreum* Marsh. Low shrubs are *Ceanothus americanus* L., *Gaylussacia dumosa* T. and G., *Rosa humilis* Marsh., and *Yucca filamentosa* L.; while common woody vines with persistent or evergreen leaves are a number of species of *Smilax* (*S. pseudochina* L., *S. bona-nox* L., *S. glauca* Walt.), *Gelsemium sempervirens* Ait., and *Lonicera sempervirens* L.

The herbaceous growth in the pine forest, when undergrowth is not disturbed, is not abundant, but in woodland burnt over or cleared, grasses and sedges spring up and often make pasturage. Blooming early in the spring, *Oxalis stricta* L., *O. corniculata* L., *Phlox pilosa* L., *Scutellaria integrifolia* L., *Salvia lyrata* L., *Houstonia purpurea* L., *Specularia perfoliata* A.DC., *Antennaria plantaginifolia* Rich., *Pyrrhopappus carolinianus* DC., and *Chrysogonum virginianum* L. are herbs which indicate xeromesophytic conditions. In more mesophytic places *Houstonia rotundifolia* Michx. and *Mitchella repens* L. may be found in bloom at almost any date, the latter with flowers and fruits at the same time.

There is no vernal flora, nor can a definite flowering season be set, but there is overlapping and irregularity in the prolongation of the blooming season, conditions related to the spring drought and to the extended growing season due to the climatic causes. The most showy season, so far as the herbs are concerned, is after the summer rains, during the late summer and the fall, when *Agrimonia Eupatoria* L., *Schrankia uncinata* Willd., *Lespedeza hirta* Ell., *L. striata* H. and A., *L. violacea* Pers., *Polygala sanguinea* L., *P. verticillata* L., *Helianthemum carolinianum* Michx., *Oenothera biennis* L., *O. linearis* Michx., *Sanicula canadensis* L., *Gentiana villosa* L., *Asclepias verticillata* L., *A. variegata* L., *Trichostema dichotomum*

L., *Salvia azurea* Lam., *Penstemon laevigatus* Ait., *Gerardia flava* L., *G. purpurea* L., *Galium circaezans* Michx., *Eupatorium coelestinum* L., *E. aromaticum* L., *E. album* L., *Liatris scariosa squarrulosa* Gray, *Chrysopsis mariana* Nutt., *Gnaphalium purpureum* L., and *Solidago petiolaris* Ait., make a representative list for the short-leaved pine wood.

The succeeding stage in upland reforestation is that of the oak-hickory forest, in which the characteristic xeromesophytic oaks are dominant. Of these two oaks, *Q. falcata* Michx. seems the more xerophytic, at least it appears on more exposed and drier situations and soils, and slightly in advance of *Q. stellata* Wang., the other pioneer oak. But together, these with *Carya alba* K. Koch dominate the forest which rapidly follows the short-leaved pines.

With the increasing mesophytic conditions (shade, humus, moisture, bacterial, and fungal development), other oaks (*Q. nigra* L., *Q. laurifolia* Michx., and *Q. alba* L.) appear. Other large trees are *Liquidamber Styraciflua* L. and *Nyssa sylvatica* Marsh. The undergrowth is composed of many seedlings of these species and others, with the small trees and shrubs common to the pine forest, as well as more mesophytic species, such as *Ostrya virginiana* K. Koch, *Cercis canadensis* L., *Aralia spinosa* L., and *Viburnum rufidulum* Raf.

The appearance of young *Magnolia grandiflora* L. and of *Fagus grandifolia caroliniana* Fernald and Rehder indicates the approach of the climax and of the transition to the magnolia-beech forest, in which the broad-leaved evergreens and a variety of deciduous trees assemble.

An undisturbed hammock forest of such mesophytic composition, and apparently representative of the climax capable of development on the uplands, contains abundant magnolias of stately proportions (60–80 ft.), equally large beeches, and Florida sugar maples (*A. floridanum* Pax or *A. saccharum floridanum* Sarg.), with intermixed live oaks, white oaks, red oaks (*Q. texana* Buckley), basket oaks (*Q. Michauxii* Nutt.), sweet gums, big bud hickories, and dogwood, with a few old and large short-leaved and Cuban pines as relics. The abundance is approximately in the order named, and all may be hung with Spanish moss. The shrubbery of

this forest includes *Asimina parviflora* Dunal, *Hamamelis virginiana* L., *Evonymus americanus* L., *Stewartia Malachodendron* L., *Aralia spinosa* L., *Symplocos tinctoria* L'Her., *Osmanthus americanus* Br., *Viburnum rufidulum* Raf., and *V. nudum* L., an assemblage of northern and southern species all about equally indicative of similarly mesophytic habitats; while perhaps the most significant thing is the occurrence of young beeches and magnolias, emphasizing the climax conditions.

The undergrowth and herbage are apparently related to the prevalence of the magnolias and other heavily foliaged trees. If these are dominant, the ground is freer of growth and covered with the heavy and slowly decaying leaves. *Mitchella repens* L. is a common floor covering. Root parasites are *Conopholis americana* Wallr. and *Epifagus virginiana* Bart.; while *Monotropa uniflora* L. and *M. Hypopitys* L. occur in abundance in the damp, shaded soil.

To summarize, the forest succession on clay soil of the upland, as shown in phases of reforestation on limited areas but in all stages, we see (1) pines, (2) oak-hickory forest, (3) deciduous broad-leaved evergreen forest. In the pine forest, *P. echinata* Mill. is the dominant species; in the oak-hickory forest, *Q. falcata* Michx. and *Q. stellata* Wang. with *C. alba* K. Koch; in the climax forest, *Magnolia grandiflora* L., *Fagus grandifolia caroliniana* Fernald and Rehder, and a variety of associates.

Sandy soils

In comparison with the uplands of the northern part of the county, those of the south seem like lowlands. Since their geological history has not been the same and the resultant topography is not so distinct, the vegetational aspect also is different. The two regions seem to exemplify two stages in the coastal plain development, the older and the younger. The southern or younger part typifies the marginal portion of the coast, of comparatively recent emergence, and belonging quite entirely to pre-erosion topography, being level, of low elevation, and covered with loose sandy deposits. Almost the whole surface, therefore, may be considered as upland.

The base leveling of this region, supposing no future oscillatory changes of importance, may require a prolonged period, the ero-

sive forces being capable of slight application, but it will not require extensive work as compared with the more elevated regions to the north. The vegetation seems naturally divided, according to small differences in elevation, into the so-called "scrub," the more or less rolling pinelands, and the flatwoods. In a general way these differences also correspond with the soil types, the scrub being associated with Sandhill soil, the pinelands with Norfolk sands, and the flatwoods with Leon sands. For convenience, these 3 general divisions of the pre-erosion uplands will be discussed separately.

SCRUB OAK FOREST.—The oak association seems to mark the sandhill areas, which, owing to the porous sandy subsoil and the lack of organic matter in the soil, would seem to be a decidedly xerophytic habitat. Three small deciduous oaks and a scattering of pines (*P. palustris* Mill. chiefly) make up the tree growth. Of these oaks, *Q. Catesbaei* Michx. seems to be the most xerophytic, as it is sometimes almost alone on the summits of the knolls or ridges. *Q. margaretta* Ashe (suggested as a possible hybrid between *Q. stellata* Wang. and *Q. alba* L. and sometimes, as noted on the more fertile soils, apparently intergrading into well grown *Q. stellata* Wang.) appears in the intermediate positions; while *Q. cinerea* Michx. grows near the bases of slopes. They intermingle in varying proportions over most of the area, growing to about the same height (15–20 ft.), with many scrubby branches, making when thickly planted a scrubby thicket. *Q. geminata* Small, a scrubby live oak, is another species occurring on sandy soil, usually in situations near water or damp places. *Q. virginiana* Mill. and *Diospyros virginiana* L. also grow on the sandhills.

Shrubs are mostly low and with evergreen or persistent foliage, as *Ceratiola ericoides* Michx., *Leiophyllum buxifolium* Ell., *Vaccinium Myrsinites* Lam., *V. stamineum* L., *V. neglectum* Fernald. *Asimina pygmaea* Dunal (with deciduous though coriaceous leaves), *Ceanothus microphyllus* Michx., and *Vaccinium tenellum* Ait. are other low shrubs of the dry sands.

The herbaceous growth, although sparsely distributed, includes a great variety of coastal plain species. Tufts of scattered wire or poverty grass occur on the spaces of bare sand, the most common

being species of *Andropogon* and of *Aristida*. *Pteris aquilina* L. is abundant also. In the spring, *Cassia Chamaecrista* L., *C. nictitans*, L., *Lupinus perennis* L., *L. villosus* Willd., *Tephrosia virginiana* Pers., *T. spicata* T. and G., *Baptisia simplicifolia* Croom, *B. lanceolata* Ell., *Euphorbia corollata* L., *E. Ipecacuanhae* L., *Croton argyranthemus* Michx., *Jatropha stimulosa* Michx., *Amsonia ciliata* Walt., *Scutellaria integrifolia* L., and *Chrysogonum virginianum* L. are early bloomers, the Leguminosae being most abundantly represented. Through the summer and fall a characteristic and representative list includes *Eriogonum tomentosum* Michx., *Eriogonum longifolium* Nutt., *Polygonella gracilis* Meisn., *Petalostemum corymbosum* Michx., *Desmodium rigidum* DC., *Rhynchosia simplicifolia* Wood, *Hypericum Drummondii* Grev. and Hook., *Angelica dentata* Coult. and Rose, *Asclepias tuberosa* L., *Verbena angustifolia* Michx., *V. caroliniana* Michx., *Gerardia fasciculata* Ell., *Elephantopus tomentosus* L., *Eupatorium aromaticum* L., *Trilisa odoratissima* Cass., *T. paniculata* Cass., *Kuhnia eupatorioides* L., *Liatris tenuifolia* Nutt., *L. elegans* Willd., *Chrysopsis graminifolia* Nutt., *C. gossypina* Nutt., *C. mariana* Nutt., *Berlandiera texana* DC., *Solidago odora* Ait., *Aster lateriflorus* Britt., *A. concolor* L., *Silphium Asteriscus* L., *Helianthus radula* T. and G., *H. mollis* Lam., and *Palafoxia integrifolia* T. and G. Many of these are perennials with prostrate or rosette-forming habit, or with pubescent to flocculent coating on leaves and stems, or, as in the case of the species of *Croton*, a scaly coating or with thick and narrow leaves.

PINELANDS.—Passing to the somewhat lower Norfolk sand, which generally surrounds the islands of Sandhill, the transition is marked by the increase in long-leaved pines. The 3 scrub oaks continue as more or less abundant members of the pine forest (fig. 2). *P. palustris* Mill. and *P. caribaea* Morelet are the pines, both of them valuable species for their turpentine and for their timber. *Quercus virginiana* Mill. and the xerophytic oak *Q. marilandica* Moench. occur occasionally, also *Q. pumila* Walt., a low, shrublike species. *Crataegus panda* Beadl., the common hawthorn of the sands in this vicinity and noticeable for its dark, deeply checked bark and irregular crooked-branched habit, and *Bumelia lanuginosa* Pers. are small trees. *Castanea pumila* Mill. is com-

mon in some places, making groves of trees or a low, shrubby growth, spreading by stolons and rapidly covering a considerable area. *Diospyros virginiana* L. is also a tree of these sands, but more frequent as second growth with the short-leaved pines, live oaks, post oaks, Spanish oaks, and sweet gums, as on cleared land which has been cultivated for a time and allowed to revert to forest.

In this reforesting the early stages thus resemble those on the hills, but to these clearings the long-leaved pines with the scrub

FIG. 2.—Long-leaved pine forest on Norfolk sand

oaks may also return. It is on such more fertile spots or where there has been improvement of the soil that the xerophytic scrub oaks, especially *Q. margaretta* Ashe, appear to grow to better size and may mingle for a time with the xeromesophytic oaks, but cannot long compete with the large trees.

The exact relation of these scrub oaks to this type of pine forest is of interest, as they sometimes appear to replace the pines without apparent difference in topography, soil, or drainage. From the fact that these oaks may appear as xerophytic pioneers, and also that they appear in the more xerophytic situations, as on the summits of the ridges of the sandy soil, it may be that they succeed

better than pines on dry, sterile sand, so that when the pines are removed from such lands, the scrub oaks more quickly take possession, while the pines return more slowly and scatteringly. On the other hand, with improved or more mesophytic conditions, the scrub oaks are soon replaced by pines, xeromesophytic oaks, and the succeeding mixed forest.

There seem, therefore, to be two possible phases of succession on the sandy soils. On the more sterile sands, the scrub oaks may be the pioneers before the long-leaved pines; or, if the pines be removed, these oaks may follow, to give place, with improvement of soil and moisture, to xeromesophytic pines and oaks, and then to the oak-hickory forest, leading toward the climax forest sooner or later. But on soil neither excessively drained nor poorly drained, the scrub oaks will accompany the long-leaved pines, yielding, where more mesophytic growth is favored, to the short-leaved pines and their following as outlined. Groves of short-leaved pines are not uncommon within the long-leaved pine association, especially where there may be some admixture of clay, as when the Norfolk sand is in close association with such types of soils as the Orangeburg and Norfolk fine sandy loams.

The growth of shrubs in these long-leaved pine woods is noticeably scanty and the species relatively few. The frequent burning over of these woods and their utilization for turpentine no doubt prevent a natural growth from starting. However, the contrast with the short-leaved pine forest on the hills is very great in this respect, and the xerophytic conditions are correspondingly greater; hence succession or the renewal of the forest is delayed. The shrubs noted commonly in the pinewoods on sandy soils are *Rhus copallina* L., *Ceanothus americanus* L., *Ilex vomitoria* Ait., *Vaccinium arboreum* Marsh., *V. virgatum* Ait., *V. stamineum* L., *V. Myrsinites* Lam., *V. neglectum* Fernald, *Leiophyllum buxifolium* Ell., *Kalmia hirsuta* Walt., and *Gaylussacia dumosa* T. and G., the Ericaceae being the most numerous. The variety of herbs in these pine forests is striking, many of them being those of the "scrub," the families prominently represented being Compositae, Leguminosae, Euphorbiaceae, Scrophulariaceae, Polygalaceae, and Labiatae, chiefly xerophytic species.

FLATWOODS.—From the dry pinewoods to the flatwoods areas the change is indicated, not by the prevailing tree growth, but by the shrubs and herbs. These mark a most decided difference (fig. 3). The long-leaved pines continue to form the forest, apparently succeeding best on these poorly drained sands. This is

FIG. 3.—In foreground saw palmettos and wire grasses and herbs characteristic of flatwoods, giving way in background to long-leaved pine-scrub oak association.

perhaps the explanation of the specific name of *Pinus palustris* Mill., although this particular pine is by no means a typical swamp tree, as for example is *P. serotina* Michx., nor is it as tolerant of inundation even for a time as is its associate *P. caribaea* Morelet.

The shrubby growth of these flatwoods is made up of dwarf species, seldom rising above 3 ft., and chiefly evergreens. Fires

may be one of the chief causes preventing development of undergrowth, but the presence of these low shrubs adjoining bays and ponds, where fires have been able to do small damage to the natural growth, seems to prove the character of the shrubbery. Dwarf oaks are common (*Q. myrtifolia* Willd., *Q. minima* Small, and *Q. nana* Willd.), with persistent, leathery leaves and mostly bearing abundant fruits. *Myrica cerifera pumila* Michx., *M. carolinensis* Mill., *Ilex glabra* Gray, *Hypericum myrtifolium* Lam., *H. galioides* Lam., *H. aspalathoides* Willd., *H. opacum* T. and G., and *Kalmia hirsuta* Walt. are other shrubs with persistent foliage. *Pyrus arbutifolia* L. f., *Rhododendron nudiflorum* Torr., *R. viscosum* Torr., *Lyonia nitida* Fernald, *Andromeda ferruginea* Walt., *Vaccinium stamineum* L., and *V. Myrsinites* Lam. are also shrubs of the damp to wet sands.

The most conspicuous index, however, of subsoil more or less saturated is *Serenoa serrulata* Hook. f. (saw palmetto). As soon as this palmetto appears with the turpentine pines, poor drainage is to be inferred. The herbs also are strikingly characteristic of undrained soil with its lack of aeration and consequently of assimilable nitrogenous substances. The Leguminosae, so abundantly represented on the Sandhill soil and in the long-leaved pinewoods on the dry sands, do not appear. Besides the grasses and Compositae, the families most in evidence here are Eriocaulaceae, Juncaceae, Liliaceae, Orchidaceae, Sarraceniaceae, Droseraceae, Polygalaceae, Melastomaceae, Onagraceae, Gentianaceae, Scrophulariaceae, and Lentibulariaceae. Representatives of these familes are *Eriocaulon decangulare* L., *E. compressum* Lam., *Juncus Elliottii* Chapm., *J. debilis* Gray, *Xerophyllum asphodeloides* Nutt., *Spiranthes praecox* Wats., *Calopogon pulchellus* R. Br., *Sarracenia flava* L., *S. psittacina* Michx., *S. Drummondii* Croom, *S. minor* Walt., *Drosera brevifolia* Pursh, *Polygala lutea* L., *Rhexia mariana* L., *R. glabella* Michx., *R. virginica* L., *R. ciliosa* Michx., *Ludvigia pilosa* Walt., *L. alternifolia* L., *Viola lanceolata* L., *Eryngium virgatum* Lam., *Sabatia Elliottii* Steud., *S. paniculata* Pursh, *Gentiana Porphyrio* G. Gmel., *Gerardia filifolia* Nutt., *Seymeria tenuifolia* Pursh, *Pinguicula lutea* Walt., *P. pumila* Michx., *Utricularia subulata* L., and *U. cornuta* Michx. The species of *Sarracenia*

are often associated with a luxuriant growth of *Lycopodium alopecuroides* L. or *L. carolinianum* L. and with beds of sphagnum and other mosses. *Osmunda cinnamomea* L., *O. regalis* L., *Onoclea sensibilis* L., *Woodwardia areolata* Moore, and *W. virginica* Sm. are typical bog hydromesophytes and abundant ferns of this habitat. A complete analysis of the flora of these low woods probably would include a longer list than for any other habitat in the county, and would be evidence of the edaphic character of this association.

Summarizing the vegetation as described for the uplands on sandy soils, the long-leaved pines are dominant and constitute the most extensive type of forest. Of these two species, *P. palustris* Mill. and *P. caribaea* Morelet, the latter ranges more widely in habitat, occurring from mesophytic to hydrophytic habitats, even enduring inundation. The former is not a typical swamp tree nor does it succeed well in soil subject to inundation for any length of time. On this account, probably, *P. caribaea* Morelet, a dominant species for the southern Florida pinewoods, is reported to be gradually replacing *P. palustris* farther north. On mesophytic soils these pines are displaced by the more mesophytic species, while on the drier soils or excessively drained sands the scrub oaks succeed better and take possession. *P. palustris* belongs typically, therefore, to sandy soils with subsoil well drained to saturated or forming hardpan, soils in which few other trees would flourish. Since such habitats predominate, owing to the present physiographic conditions on the coastal plain, the present long-leaved pine forest may be looked upon as edaphic, the species of pines, within their respective climatic ranges, being pioneers in these comparatively primitive habitats.

PRE-EROSION DEPRESSIONS

Throughout the coastal plain, depressions not resulting from recent erosive processes present a variety of edaphic studies. Many of these low places are filled for all or part of the time with surface water, or they may be sufficiently depressed below the water table to contain a permanent amount of water. Others may be mere swampy or boggy tracts, or during dry seasons prairie-like. The relation of these surface features to the formation of peat,

especially in Florida, has been investigated and reported by HARPER (6), whose descriptive classification of habitats and extensive lists of peat-forming plants present a summary of the plant associations of the various sorts of swamps, marshes, bogs, ponds, lakes, and streams.

The water of these pre-erosion depressions, with their (usually) sandy basins, is characteristically dark-colored, appearing blackish when in quantity, being rich in organic matter, and having a more or less acid reaction.

Lakes, ponds, and streams

The vegetation of the ponds and of the slowly moving waters of the sluggish little streams is not decidedly different, differences depending rather on the depth of water and on the amount of movement. In shallow, permanent water the aquatics are arranged in the usual zonation, from those submerged or floating to those rooted in the muck or sand of the bottoms and to the amphibious plants of the margins.

Lists of aquatics for the ponds and lakes include among the submerged and floating forms *Potamogeton* spp., *Ceratophyllum demersum* L., *Myriophyllum heterophyllum* Michx., *Lemna valdiviana* Philippi, *Castalia odorata* Woodv. and Wood (and the variety *C. odorata gigantea* Fernald), *Nymphaea advena* Ait., *Brasenia Schreiberi* Gmel., *Nelumbo lutea* Pers., *Nymphoides aquaticum* Fernald, *Utricularia inflata* Walt., *U. biflora* Lam., and *U. purpurea* Walt.

In marginal zones, *Panicum hemitomum* Schult., *P. condensum* Nash, *Dulichium arundinaceum* Britt., *Eriocaulon decangulare* L., *E. compressum* Lam., *Mayaca Aubleti* Michx., and *Bacopa caroliniana* Robinson usually grow in shallow water; while the common strand plants are *Fuirena squarrosa* Michx., *Hemicarpha micrantha* Britt., *Rhynchospora corniculata* Gray, *Syngonanthus flavidulus* Ruhland, *Drosera brevifolia* Pursh, *Hypericum virginicum* L., *H. gentianoides* BSP., *Hydrocotyle umbellata* L., *Bartonia* spp., *Diodia virginiana* L., *D. tetragona* Walt., *Spermacoce parviflora* Gray, *Houstonia angustifolia* Michx., *Lobelia glandulosa* Walt., and *Pluchea foetida* DC. The cypresses (*Taxodium distichum* Rich. or

T. distichum imbricarium Sarg.) when present are the chief tree pioneers in the ponds, advancing farthest into the deeper water, reaching from the zone of high water, perhaps, to the extreme limit of the occasional low water, into the zone of water lilies and submerged aquatics (fig. 4). *Cephalanthus occidentalis* L. is a close companion of the cypresses and advances into the standing water

FIG. 4.—Cypresses advancing into deeper water

as a shrub pioneer. The hydrophytic species of *Nyssa* (*N. aquatica* L., *N. sylvatica biflora* Sarg., and the less frequent or local *N. Ogechee* Marsh.), germinating and growing in shallow water, may accompany the cypresses or may spread over the shallow ponds to form the so-called "gum swamps" (fig. 5).

Approaching the shores or in the shallow water of the margins, these trees are joined or surrounded by a zone of marginal shrubs and small trees. Among those which commonly grow in this zone are *Salix longipes* Anders., *Magnolia virginiana* L., *Persea pubescens*

Sarg., *Crataegus viridis* L., *C. aestivalis* T. and G., *Cyrilla racemiflora* L., *Cliftonia monophylla* Britt., *Ilex Cassine myrtifolia* Sarg., *Acer rubrum* L., *A. rubrum tridens* Wood, *Hypericum fasciculatum*

FIG. 5.—Gums (*Nyssa* spp.) forming a gum swamp; trees show swollen bases, and a seedling in center of picture has germinated and is growing in the dark water.

Lam., *H. myrtifolium* Lam., *H. microsepalum* Gray, *Lyonia nitida* Fernald, and *Leucothoe racemosa* Gray.

On the edge of moist but not inundated soil, species of *Myrica* may grow, while *Serenoa serrulata* Hook. and *Ilex glabra* Gray mark

the line of high water. Here live oaks, water oaks, sweet gums, and the swamp and pond pines appear, beginning a meadow or swamp, or quickly giving way to the immediate upland climax (fig. 6). *Smilax Walteri* Pursh is the liana significant of inundated soil, while *S. laurifolia* L. and *S. lanceolata* L. are marginal lianas on moist soil.

FIG. 6.—Lake margin, showing cypresses in water, shrub zone within range of high water, and live oaks on rising ground.

Ponds which dry out during the season are often encircled by hawthorns, *C. viridis* L. being a common marginal species, and *C. aestivalis* T. and G. may fill a shallow or transient pond and convert it into a "mayhaw pond." On areas of clayey soils, willows, maples, sweet gums, and button bushes are the commoner marginal trees and shrubs; while the chief variations in ponds on sandy soils are due to the presence of cypresses or of gums as the tree pioneers,

the composition of the shrubbery about the margin, and in succeeding climax.

Pre-erosion streams, being slow and shallow, do not differ much from the ponds as described. The aquatics in moving water are not so numerous, but the shore growth is more varied, and may grade, with the drainage, into bordering strips of meadow on lowland hammock by which the streamways are conspicuously marked from the adjoining pine forests.

Waters flowing from limestone springs and which are clear and more calcareous have a somewhat different vegetation from that of the acid, brown waters of the other streams. *Liquidambar Styraciflua* L. is a tree of the sometimes inundated margins, and *Ulmus americana* L., *Fraxinus caroliniana* Mill., *F. profunda* Bush, *Quercus nigra* L., *Salix longipes* Britton, *Acer rubrum* L., *Ilex Cassine* L., *Cornus stricta* Lam., and *Cephalanthus occidentalis* L. are common. Canes (*Arundinaria tecta* Muhl.), reeds (*Phragmites communis* Trin.), and saw grass (*Cladium jamaicense* Crantz), with bulrushes (*Scirpus* spp.) are marginal marsh plants.

Swamps and meadows

FLOWING WATERS.—Swampy borders of varying width or overflow strips of meadow are the almost invariable accompaniment of pre-erosion branches, creeks, and rivers, the width of the overflow area depending upon the topography and upon the consequent drainage basin, and upon the volume of the stream. By the accumulation of humus and as improved drainage is secured, these meadow areas in many cases tend to extend outward or upward and often come to occupy wider spaces than would be explained solely by the fluctuations of the stream. From the adjoining vegetation they are marked off by species ranging from hydrophytic to extremely mesophytic. The swampy character extends as far as the soil continues saturated, and in this zone there occur trees of the pond margins, such as cypresses, gums, willows, birches, ashes, water hickory, and water elm (*Planera aquatica* J. F. Gmel.).

On slightly rising ground, but still within range of the high water, there occur pines (*P. caribaea* Morelet, *P. serotina* Michx., *P. palustris* Mill., and *P. glabra* Walt.), with a variety of oaks, such

as *Q. nigra* L., *Q. laurifolia* Michx., *Q. Michauxii* Nutt., also *Carpinus caroliniana* Walt. and *Liquidambar Styraciflua* L. (fig. 7).

Many shrubs and small trees belong to these swampy margins, making a dense growth to the water's edge, with intermingling

FIG. 7.—Exterior view of Ocklocknee River meadow, showing dense deciduous growth at swampy edges; pines coming in on higher ground.

myricas, bays, and mixed shrubbery, among which are *Itea virginica* L., *Rhus Vernix* L., *Cyrilla racemiflora* L., *C. parvifolia* Raf., *Sebastiana ligustrina* Mill., *Ilex Cassine* L., *I. decidua* Walt., *Cornus stricta* Lam., *Clethra alnifolia* L., *Rhododendron* spp., *Andromeda ferruginea* Walt., *Cephalanthus occidentalis* L., *Pinckneya pubens*

Michx.; with also a variety of lianas such as *Smilax Walteri* Pursh, *S. laurifolia* L., *Berchemia scandens* Trel., *Trachelospermum difforme* Gray, and *Aster carolinianus* Walt.

Beyond reach of frequent inundations, in soil enriched by accumulation of humus, the most mesophytic stage is reached, and the meadow grades into the lowland or river hammock, where a mixed forest of many species develops. *Fagus grandifolia caroliniana* Fernald and Rehder and *Magnolia grandiflora* L. may appear here, with *Celtis mississippiensis* Bosc., *Liriodendron Tulipifera* L., *Halesia carolina* L., *H. diptera* Ell., *Chionanthus virginica* L., and others, forming rich forests of varying composition along the streams. In these forests is an assemblage of mesophytic shrubs, such as *Alnus rugosa* Spreng., *Hamamelis virginiana* L., *Aesculus Pavia* L., *Styrax* spp., and *Viburnum* spp., with lianas and climbing shrubs, such as *Decumaria barbara* L., *Wistaria frutescens* Poir., *Sageretia Michauxii* Brong., *Rhus Toxicodendron* L., *Psedera quinquefolia* Greene, *Cissus Ampelopsis* Pers., *Cissus arborea* Des Moulins, *Vitis rotundifolia* Michx., *V. aestivalis* Michx., *Bignonia capreolata* L., *Tecoma radicans* Juss., and the mesophytic species of *Smilax*. Ferns of the swampy or wetter soils are *Osmunda* spp., *Onoclea sensibilis* L., and *Woodwardia* spp. Of more mesophytic habit are *Aspidium Thelypteris* Sw., *A. patens* Sw., and *Asplenium Filix-femina* Bernh. On the water oaks, black gums, and various other trees *Phoradendron flavescens* Nutt. is abundant, and also *Tillandsia usneoides* L., the ever common epiphyte.

It is to be noted that the character of a well developed stream or river hammock of the region is quite the same wherever occurring and within the boundaries of whatever soils. The telescoping of swamp and hammock complicates the successional phases and is usually extreme, since even slight differences in elevation or drainage are sufficient to modify the vegetation extensively.

QUIET WATERS.—The so-called "bays" are examples of shallow undrained swamps supporting a more or less dense growth of shrubs or small trees. *Magnolia virginiana* L., *Persea pubescens* Sarg., and *P. Borbonia* Spreng. are the real "bays," but the list of plants for these boggy ponds includes a variety of other species, as cyrillas,

grapes, hollies, hypericums, hawthorns, and ericads, and such trees as cypresses, gums, and slash and swamp pines.

There is little suggestion of any definite succession in the composition of the bay or similar swamp. However, *Magnolia virginiana* L., *Persea pubescens* Sarg., and *Ilex Cassine myrtifolia* Sarg. seem to advance into the more hydrophytic portions and appear near the center of the swamp surrounded or followed by the grapes, ericads, and myricas; while *Ilex glabra* Gray, *I. lucida* T. and G., and *Serenoa serrulata* Hook., with *Hypericum* spp. grow beyond the standing water. Frequently *Ilex Cassine myrtifolia* Sarg. is so abundant as to make a fairly impenetrable thicket.

FIG. 8.—Cypresses advancing into waters of an undrained pond, gradually forming a cypress swamp.

An undrained pond may develop into a cypress swamp, the cypresses growing as closely as their swollen bases and groups of projecting knees permit (fig. 8). Around the margin of such a swamp there may be a mingling of oaks, gums, and pines, but more frequently there is a sharp transition to the forest of the upland adjacent, and the edge of the swamp is abruptly marked by the ranks of flat-topped cypresses. When the gums mingle with the cypresses or are the most abundant or only trees, a gum swamp develops, these trees also having swollen or bulging bases. *Tillandsia usneoides* L. gives a characteristic touch to their appearance, especially in winter when the trees are leafless.

The herbs of such swamps are mainly those of pond margins and of the flatwoods, as *Panicum hemitomum* Schutts, *P. condensum* Nash, *Aristida spiciformis* Ell., *Eleocharis* spp., *Fuirena squarrosa* Michx., *Rhynchospora* spp., *Eriocaulon* spp., *Mayaca Aubleti* Michx., *Burmannia biflora* L., *Polygala cymosa* Walt., *P. ramosa* Ell., *Hypericum petiolatum* Walt., *H. virginicum* L., *Ludvigia alternifolia* L., *L. glandulosa* Walt., *Gerardia linifolia* Nutt., *Lobelia amoena* Michx., and *L. glandulosa* Walt.

In certain low places, as at the bases of slopes, water may ooze through the sandy soil to collect on the surface in little pools or pockets, with intervening hammocks of dark muck, or may slowly drain away, sometimes forming the source of a small stream. In this way small branches or considerable tributaries may originate, and by their union form creeks or small rivers. In other cases sloughs and ponds may be formed, such boggy spots often being designated "galls." In vegetation they resemble the bays, often surrounded by or advancing to a hammock stage by the accumulation of humus and the gradual building up of the soil.

Bayheads scarcely differ from these, also being the sources of small branches. In these, typical trees are *Magnolia virginiana* L. and *Persea pubescens* Sarg., with a bordering shrubbery of more or less mesophytic character.

Sloughs are low, flat passageways between swamps or bodies of water. In these passageways the water may be still or but slowly moving, while during the dry season they may be entirely dried out. Cypresses, sour gums, swamp pines, and swamp maples are common slough trees, with live oaks, water oaks, holly, and sweet gums on the edges. Swamp shrubs, including a variety of the ericads, cyrillas, gallberries, hypericums, with the saw palmetto, out of reach of the standing water, are numerous.

Prairies

Prairies are comparable to swamps in being depressions below the general surface and lacking surface drainage. They may be flooded during the rainy seasons and dry at other times, and their vegetation consists typically of herbaceous associations, especially the grasses. No extensive natural prairies exist in connection with the pre-erosion topography under description here, although many of the small ponds and lakes may temporarily become prairie-like, their beds during the dry seasons being overgrown with grasses and other herbage, in which introduced plants, as weeds, make a miscellaneous assemblage.

EROSION TOPOGRAPHY

The northern part of Leon County, having been exposed probably as long as any other section of Florida or of the immediate Gulf

Coast, and being in parts above the general level, should afford illustrations of erosion topography. The conditions are unusual, however, since the presence of limestone so near to the surface has brought about the development of extensive subterranean as well as surface erosion, and the topographic features are thus modified in such ways as to complicate ecological analysis. In considering the region as a whole, it appears that the surface features may be largely due to the underground erosion. The lakes, sinkholes, and enclosed valleys seem evidence of this.

Surface erosion

BRANCHES AND CREEKS.—The trough of almost every valley has a waterway marked by an aggregation of trees and shrubs. The stream is usually an insignificant affair so far as the amount of movement of the water is concerned, and consequently the erosive work accomplished by such a stream is slight. Its course may be found to lead, by a slight rise, to a bayhead where the water is seeping from the base of a slope; or it may issue from a spring whence the water may flow across the ground, spreading out into a miry tract; or, as in the clayey soil of the hills, a definite channel will be cut or gullied down the slope; or the spring will eat back into the hill as a narrow ravine and a small clay canyon thus be cut along the steeper part of the grade. The erosion work lessens as the level is reached, the washing and gullying of the steep banks grade and widen them, and in this way the little streams are gradually bringing the soils of the hills to the valleys.

RAVINES.—In the shady and moist ravines there grow numerous liverworts and mosses, with soil lichens in the upper zone and with ferns along the edges and in the niches. Of the ferns, *Polypodium polypdioides* Hitch. grows on the moist clay banks, also *Asplenium platyneuron* Oakes, *A. resiliens* Kunze., *Polystichum acrostichoides* Schott., *Aspidium Thelypteris* Sw., and *A. patens* Sw. As the stream broadens and shallows and the banks are lowered, reeds, canes, and marsh grasses border the edges, while trees and shrubs develop to form a meadow hammock.

RIVERS.—The Ocklocknee River is an example of an extended stream, rising in Georgia and cutting its way across the latest

deposits of the coast. For most of its course along the western border of Leon County its banks are edged by bluffs of varying elevation (50–100 ft. above sea-level). These are apparently the ancient banks, eroded during a previous period. At places these bluffs approach close to the present low banks, so that the valley varies in width. The erosion work of the river is of small importance, and in its bordering meadow and overflow land it resembles a pre-erosion stream. The low bluffs are generally well wooded and the undergrwoth is often denser and of a more mesophytic type than is that of the upland forest.

Examples of small erosion creeks are to be seen in the southwestern edge of the county, where a series of drainage streams flow from the bays on the Leon sand across the strip of Norfolk sand to empty into the Ocklocknee River, and have cut ravine-like valleys in the sands, in which the most mesophytic trees, including *Magnolia grandiflora* L., *Fagus grandifolia caroliniana* Fernald and Rehder, *Liriodendron Tulipifera* L., *Carya alba* K. Koch, *Acer* spp., *Carpinus caroliniana* Walt., and *Prunus caroliniana* Mill., grow with a rich undergrowth. Entering one of these eroded valleys from the upland of monotonous pine forests, one witnesses the extremes which the region can support.

LAKES.—The surface erosion along the shores of the larger lakes is of small importance, as the shores are usually sloping and the wave action is slight. The trees of the uplands may extend to the water's edge or there may be tracts of fine hammock forest. Other lakes resemble slow fluctuating streams, with cypresses in the shallow water.

Subterranean erosion

The underground solution and the resultant caving in or settling of the ground surface continue to play a part in modifying the topography.

SINKHOLES.—The formation of sinkholes may take place suddenly and expose the limestone, forming depressions, usually circular, varying in size and depth. In case there is no opening through which the water may reach an underground channel, the rainfall and the surface waters may accumulate to form a pond.

In such sinks the water rises and falls with the amount of precipitation and surface drainage. Other sinks are dry, having one or more openings in connection with the underground drainage system.

The cliffs and ledges of limestone, if exposed, soon wear off, soil collects, and gradually the sides become overgrown. The soil collecting in the bottom supports growth of trees and shrubs usually more mesophytic than those of the immediate upland, the shade and the moisture favoring the growth of such seedlings. Liverworts and mosses may be found on the damp soil at the base of a sink and often in the crevices of the sides. *Adiantum capillus-veneris* L. belongs to such situations, as also *Polypodium polypodioides* Hitchc., *Asplenium platyneuron* Oakes, and *Polystichum acrostichoides* Schott. *Panicum dichotomum* L. and *Opelismenus setarius* L. are grasses in the shady ravine-like situations, as pioneers on the sides.

If the sink contains water, pond plants will enter and cypresses or gums may grow. If the base is covered or finally filled with soil, water oaks, live oaks, sweet gums, dogwood, and holly are common sinkhole plants. White oaks, red maples, black gums, and sweet gums are other trees occurring about the sinkhole margins.

Springs.—Many springs are the results of channels in the limestones, occurring where the streams emerge from underground. In the clear, cool, calcareous water of such springs there is not much plant growth, although around the margins are grasses, sedges, sagittarias, and reeds.

Lakes and ponds.—The relation of the large lakes to sinkhole formation has been mentioned, sinks or openings occurring in their basins through which the more or less complete drainage of the waters of the lake may take place suddenly or gradually. When these sinks become closed by obstructions or stoppage, the water will again fill the basins (12). By the drainage of such lakes, sometimes large areas of the basins may become prairies, which unless again flooded or otherwise used, may gradually approach the forest stage.

Streams.—Underground channels sometimes become surface streams by the caving in of the roof of the cavern. Frequently a section may be left to form a natural bridge. Such is the case

with the St. Mark's River, which emerges from a subterranean course as a series of sinklike ponds, and finally as a surface stream flowing across the sands to the Gulf. At the natural bridge the banks are definite and rise directly from the water level. A rich hammock borders the banks, the trees and shrubs growing close to the water's edge.

Summary

This local study of the Gulf section of the coastal plain may serve to suggest several points in the successional history of the plant associations of the region. Extremes of xerophytic, hydrophytic, and mesophytic societies are to be found. The most xerophytic association is represented by the long-leaved pine-scrub oak forest of sterile, sandy soil. The most mesophytic association is that of the hammocks, occurring on the upland as the climax and also as a temporary climax in the river valleys, being composed of a large variety of species, deciduous and evergreen, of which *Fagus grandifolia caroliniana* Fernald and Rehder is perhaps the most significant deciduous tree, and *Magnolia grandiflora* L. the principal tree among the broad-leaved evergreens. Between these two extremes are the gradations from pioneer pines through the pine-oak and oak-hickory stages. Telescoping and rapid growth in the later stages are characteristic and confusing.

The long-leaved pine-saw palmetto association on the flat, poorly drained sands presents a large edaphic problem. With improvement in drainage, aeration of the soil, and consequent promotion of soil organisms and their work, the change to a mixed forest can take place, as is seen along the streams as well as in local hammocks which have evidently been built up gradually. Drainage of the subsoil brings scrub oaks in place of the saw palmetto into association with the long-leaved pines, and the succession outlined from dry pine woods to the climax forest will naturally follow. With slight depression of the surface a change to a moorlike swamp results.

The various types of swamps, characterized by the prevailing species, as the cypress swamps, gum bogs, pine swamps, and bays, and their transitions to the surrounding forest, furnish opportunities for intensive studies.

Comparative observations

In considering the upland forests in their successional stages, data concerning the evaporation, soil moisture, and certain climatic factors, and their relation to the associations discussed, have been collected. Evaporation records were secured by the use of Livingston atmometers, following the investigations of FULLER (4) and others. Rain-correcting valves were used, the cups were kept standardized to the same unit, and computations made accordingly.

Stations were established in a mesophytic forest of the climax type, in a Spanish oak-post oak-hickory forest, in a short-leaved pine forest, in a beech opening in the short-leaved pine forest, in the dry pine woods (long-leaved pines), in the scrub oaks association, and in the flatwoods. Meadow stations were also placed, but their records are not complete. The stations were located in as nearly typical situations as possible, the atmometers in each case being placed at the surface of the ground. All records demonstrate a constantly high evaporation as one of the climatic results, and all show a general relation between the evaporation and precipitation periods, there being two marked maxima for all the stations, the major one being between the winter and the summer rainfall, corresponding to the April and early May dry season, the other evident in late September and early October, after the summer rains have ceased. All records show a sudden rise in spring from the lowest point in December or January to the April or May maximum (June for the long-leaved pine forest). This corresponds generally to the period of the vernation of the deciduous species and to the renewal of foliage by many of the evergreens. Winter records for the highland stations were uninterrupted by frost through two consecutive winters, but each lowland station suffered once or twice each winter.

Of the upland stations, the average daily evaporation is lowest for the mesophytic climax (magnolia-beech) forest, being 8.5 cc. daily, estimated for a period during which an unbroken record was obtained from December 24 to May 1; this is the most critical period, including from the January minimum to the April maximum. For the same period of time the Spanish oak-post oak forest gave

a record of 9.9 cc.; the beechwood 11.21 cc.; the short-leaved pines 11.67 cc.; the long-leaved pines on Norfolk sand 12.28 cc.; and the scrub oaks 15.3 cc. daily, the reverse of this order being essentially that in which the successional changes as observed occur, from the xerophytic pines and oaks through the xeromesophytic pines and oaks to the climax forest (fig. 9). The beech wood, it must be noted, was subject to pasturing and gave evidence of

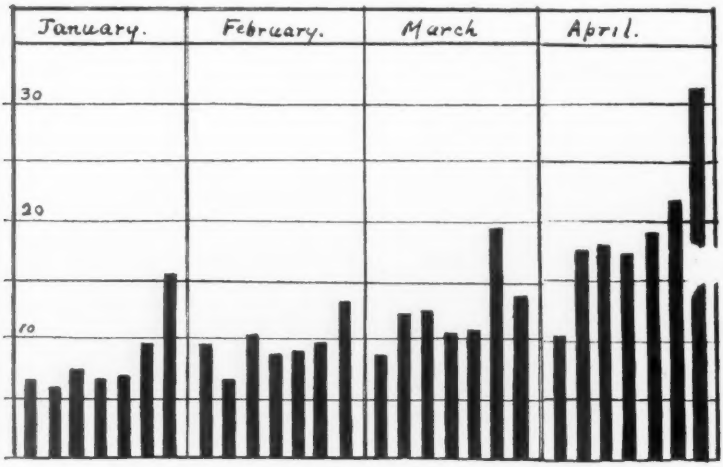

FIG. 9.—Diagram showing comparison in evaporation rate from January to May in (1) mesophytic climax forest; (2) flatwoods; (3) Spanish oak-post oak-hickory forest; (4) short-leaved pine forest; (5) pastured beech forest; (6) scrub oak forest; (7) long-leaved pine forest.

recent burning (probably to promote pasturage), being quite free of undergrowth. Cattle and hogs grazed through this forest and *Erechtites hieracifolia* Raf. appeared among the herbs.

On the basis, however, of the average rate of evaporation estimated for the year, the order is changed. The Spanish oak-post oak association has an evaporation rate very close to that of the short-leaved pines, being 14.00 cc. daily for the former and 14.22 cc. for the latter. Both of these stations were observed without a break from September 1912 to May 17, 1914, and their averages taken accordingly. The two stations are alike in that each has

a dense undergrowth, that of the pine woods being if anything denser than that of the oak forest; indeed, the pine forest is well on its way toward the oak stage. However, there is a difference when the winter and the summer averages are considered. Estimated for the period from June to November, the season during which full foliage of deciduous trees is a large factor, the daily rate for the oaks is 12.49 cc. and for the pines 13.8 cc. In winter (November to June), from the time when the oaks are leafless until they attain full summer foliage, the rates are 15.69 cc. daily for the oaks and 13.70 cc. for the pines. In the beech woods during these seasons, the rates are 13.4 cc. daily for the summer and 17.8 cc. daily for winter, thus showing an approximation to the pines in summer and greater evaporation than either pines or oaks in winter.

The scrub oaks and long-leaved pines behave differently. These oaks average 13.95 cc. for summer (comparable to the short-leaved pines and the open beech woods) and 14.1 cc. for winter; while the long-leaved pines on dry sand show the highest rates, 18.25 cc. for summer and 19.2 cc. daily for winter. The scrub oaks and the long-leaved pines have respectively 15.52 cc. and 17.9 cc. daily average for a period of 18 consecutive months. The scrub oak forest shows less actual variation than any other except the flatwoods, this probably being related to the stunted character of the oaks, their close thicket-like growth, and their habit of retaining the dead leaves most of the winter or until fresh growth starts. In striking contrast, the long-leaved pine forest shows the most extreme variations in range of evaporation of any other station.

The contrast between the two long-leaved pine associations is the greatest of any, as the flatwoods station shows a uniformly lower rate throughout the year than any other and averages 12.99 cc. daily for the 18 months, thus taking the place next in order to the mesophytic climax forest. The summer evaporation for the flatwoods averages 13.24 cc. daily, comparable to that of the scrub oaks and the pastured beech wood. The average winter rate is 11.17 cc. daily, being the lowest, and this is the case although this forest is even more open than any of the others, the shrubs being low and the forest subject to turpentining, burning, and pasturing.

Some experiments to determine the soil moisture relations (by use of the wilting coefficient) were obtained and determined according to the method of BRIGGS and SHANTZ (2). Although incomplete, these tend to confirm the statement that the flatwoods have

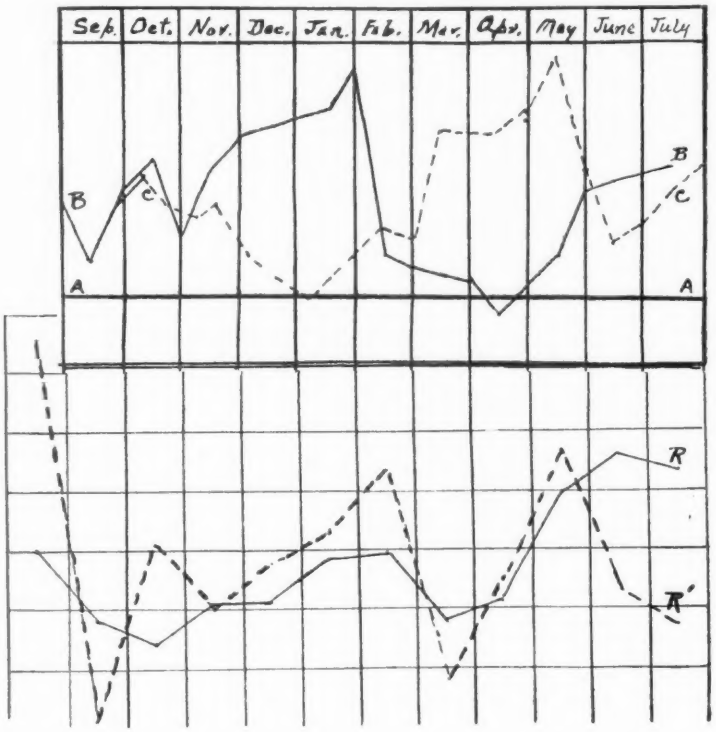

FIG. 10.—Chart showing relation of wilting coefficient and soil moisture of Leon sand, and comparison with precipitation: *AA*, wilting coefficient; *BB*, range of soil moisture from September to June; *CC*, graph of daily evaporation at flatwoods station during same period; *R*, curve of average monthly rainfall (in inches); *R'*, curve of rainfall during the period.

the wettest soil, not actual swamp, in the region. The wilting coefficient of soil taken from the first 3 inches of the surface is approximately 5.9, while the average percentage of the soil moisture present during the year is 12.74 (fig. 10). Only once (in April),

at the end of the spring drought, does the percentage of moisture in the first 3 inches of soil fall lower than the wilting coefficient, and then but slightly. The maximum amount is reached in late January and early February, while a summer maximum is reached in July, coinciding with the two periods of rainfall. The curve of the range of the soil moisture agrees quite closely with that of the average daily evaporation, which in this association therefore has a direct relation to the soil moisture and the consequent humidity of the atmosphere at the surface of the soil where evaporation is actively occurring.

Considering the edaphic character of the flatwoods in explanation of its position as determined by the evaporation averages, the order of succession for upland forests as observed seems to have a definite relation to the obtained rate of evaporation. This tends to confirm the observation that in the coastal region studied the present pines are pioneers making a temporary forest, which, owing to present geological, topographical, and soil conditions, may make but slow progress toward the ultimate climax, at least over large areas. When once started, however, the climate favors a rapid mesophytic advance.

To the lectures and teaching of Dr. H. C. COWLES I am indebted for my interest in this subject and for my point of view; to Dr. G. D. FULLER for instructions concerning field work with evaporimeters; and to Dr. J. M. GREENMAN for aid in identification of various plants. Also I acknowledge the assistance of Professor JEROME MCNEILL of Tallahassee, Florida, in the field work and in securing the evaporation and soil moisture readings over an extended time.

RICHMOND, IND.

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PERMEABILITY OF CERTAIN PLANT MEMBRANES TO WATER

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 230

F. E. DENNY

(WITH TWO FIGURES)

Introduction

In the exchange of material between the plant and its environment, 3 groups of substances may be considered important, namely, water, gases, and salts. These enter the plant, pass from one portion to another, and some of this material finally passes out into the environment again. In this process a great many membranes must be penetrated. The permeability of these membranes, therefore, is a factor in this material exchange, determining in a measure what substances may enter or leave the plant and at what rate this entrance or exit can take place. For this reason measurements of the permeability of plant membranes become desirable. While much work has been done toward this end from a qualitative standpoint, and while many indirect measurements have been made, direct quantitative measurements in which the results could be referred to known areas of membranes, under a standard set of conditions, have been lacking.

This paper deals with an attempt to get quantitative data on the permeability of certain plant membranes to water; to determine what laws, if any, hold for the rate of penetration of water as related (1) to temperature, (2) to direction of flow through membranes, (3) to concentration of the bathing solutions, and (4) to species of plant under consideration.

Membranes

Non-living membranes such as seed coats and the outer scale of the onion bulb were used, as they were suitable for use with the apparatus employed. The importance of non-living membranes

must not be underestimated. That they perform great physiological functions is coming to be recognized more and more as our knowledge of them increases.

The cell wall may be thought of as a non-living membrane, and its functional importance is emphasized by the work of HANSTEEN-CRANNER (**16**), in which it is indicated that the antagonism of $Ca^{\cdot\cdot}$ for $Mg^{\cdot\cdot}$ in root toxicity, the action of $Ca^{\cdot\cdot}$ in increasing transpiration and decreasing absorption, and the action of $K^{\cdot}$ in decreasing transpiration and increasing absorption, is due fundamentally to the effect of these ions upon the cell wall. The importance ascribed by WÄCHTER (**30**) to the cuticle and cork of the outer layers of the beet in preventing the loss of sugar also may be pointed out. Other investigators (**4, 10**) have shown that the non-living coat plays a dominant rôle in seeds, the coat character being an important factor in determining the respiration, water intake, entrance of toxic materials, delay in germination, longevity, protection from leaching of stored materials, and from mechanical injury, etc.

A study of the permeability of such membranes is desirable in itself, and it was hoped that results so obtained would throw light upon the problem of the permeability of plant membranes in general. In this connection we quote PFEFFER (**24**): "the physiological process itself will first have to deal with the experimental study of lifeless material, studies which may perhaps in their turn make clear processes taking place in the organism."

A non-living semipermeable plant membrane was discovered in 1907 by BROWN (**5**) in the barley grain, and later BROWN and WORLEY (**6**) measured its permeability to water. SCHROEDER (**27**) reported a similar membrane in the wheat grain. GOLA (**13**) found such membranes in the seeds of a great many different species. SCHROEDER and GOLA did not measure the permeability of the membranes to water. SHULL (**28**) found that the seed coat of *Xanthium* is semipermeable to certain substances, and pointed out the distinct advantage this membrane had for experimental purposes, in that it could be removed from the seed, and its permeability characters studied directly, without other structures becoming factors in the experiment. He constructed an osmometer

in which a portion of the seed coat was used as the membrane, and made preliminary measurements on the rate of penetration of water. The problem of getting quantitative measurements of the permeability of various plant membranes was then undertaken by the writer with the results here reported.

The rate of penetration of water through membranes was measured with an osmometer of the design shown in figs. 1 and 2. *A*, *B*, and *C* are hard rubber discs, 3.5 cm. in diameter and 2 mm. in thickness. Brass discs also were used, but are not suitable for

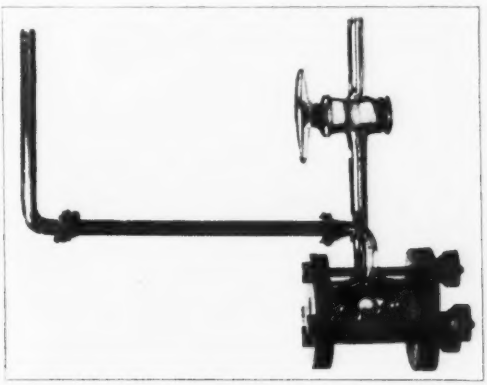

FIG. 1.—Photograph of osmometer: explanation in text

use with salt solutions. In the centers of *A* and *B* at *K* is a hole of known diameter. Between *A* and *B* and over this hole the membrane to be studied is placed; thus the area of the membrane used can be calculated. *D* is a hard glass cylinder with ground edges fitting snugly against the hard rubber discs. Soft rubber gaskets are interposed between the glass cylinder and the discs at *E*, and the apparatus made tight by screwing up the bolts at *H*. F is the tube for admitting water into the internal chamber. The latter is filled with distilled water until water appears in the horizontal capillary tube. The position of the meniscus in *G* may be set at any desired spot by means of the stopcock in *F*. *G* is a capillary tube with about 10 cm. horizontal length and with a capillary bore of approximately 1 mm. Scale divisions on *G* were

calibrated by weighing with mercury. One scale division on G = 0.000337 gm. of water at 25° C. The whole apparatus is then immersed in a vessel containing a solution of cane sugar or sodium chloride and the vessel placed in a water bath regulated to constant temperature. The osmotic force of the bathing solution pulls water through the membrane from the internal chamber, and this causes the meniscus in the capillary tube to recede. By successive

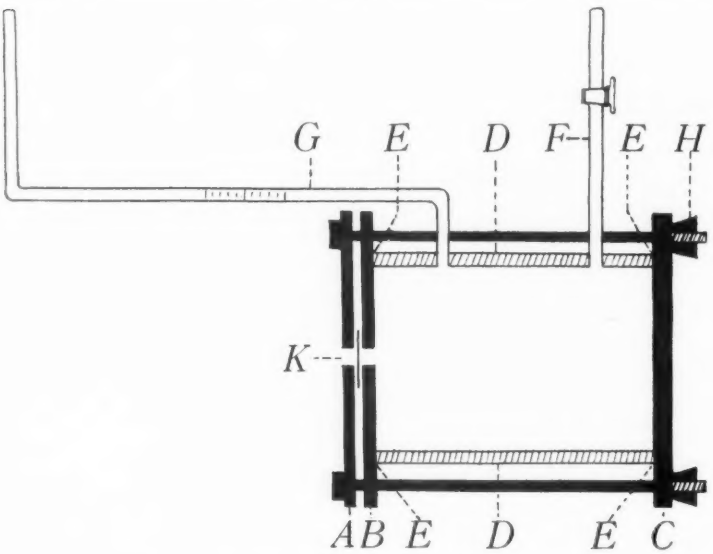

FIG. 2.—Drawing of osmometer: explanation in text

readings of the position of the meniscus in G at various intervals of time the rate of water movement through the membrane can be determined.

As water passes through the membrane, it has a tendency to dilute the bathing solution at K. This tendency is overcome by a stirrer whirling in front of the membrane at K which keeps the concentration constant there. The amount of water passing into the bathing solution is so small as compared with the large volume of the latter that the concentration of the solution exerting the osmotic pull is maintained constant.

At the end of an experiment it is possible to record the quantity of water passing through a known area of membrane, in a known interval of time, at a constant known temperature, and under the constant osmotic pull of a solution whose osmotic pressure in atmospheres is known. This gives a measure of the permeability of the membrane under the conditions of the experiment.

The sources of error and the precautions taken were as follows:

Temperature errors.—It was found that when the apparatus was immersed in the bathing solution it reached the temperature of the latter in 6–8 minutes. An interval of at least 10 minutes was allowed before readings were begun. The temperature of the bathing solution was constant to $\pm 0.^{\circ}1$ C. The effect of the possible deviation of the temperature of the internal liquid upon the readings of the meniscus in the side arm was calculated.[1] The volume of the osmometer is 4421.13 cu. mm. Assuming it filled with water at 4° C., then changes in temperature of $0.^{\circ}1$ show the relation between temperature errors and scale division of the osmometer as indicated in table I.

TABLE I

Temperature	Volume error (in mg.) of water	Scale division value (in mg.) of water	Error of readings in scale divisions
$5^{\circ} \pm 0.^{\circ}1$	0.01326	0.338	<1
$15^{\circ} \pm 0.^{\circ}1$	0.17065	0.3378	<1
$25^{\circ} \pm 0.^{\circ}1$	0.18525	0.337	<1
$35^{\circ} \pm 0.^{\circ}1$	0.30704	0.336	<1
$45^{\circ} \pm 0.^{\circ}1$	0.37212	0.3347	1.11

Accurate readings of the side arm could be made only to one scale division. Temperature deviation therefore introduced no error except at temperature as high as 45°, and then only a slight error resulted.

Variation in membranes.—It was early found that there was a large variation in the permeability of different membranes of the same species. One membrane could not be compared with another, but only with itself under the various conditions of the experiment.

[1] Calculated from data taken from Smithsonian tables, Smithsonian Misc. Coll. **63**: no. 6.

The permeability of the same individual membrane was measured under the different conditions studied, therefore, and the same set of observations made with a number of other membranes of the same species. In some cases it was possible to allow the same membrane to remain in the osmometer during a whole series of readings. When it was necessary to remove the membrane from the osmometer, care was taken in replacing it that the same portion of the membrane was used in the next reading.

Constancy of semipermeability.—When a membrane gave constant rates for 1 hour, readings being taken at intervals of 10 minutes, it was assumed that its permeability to salt or sugar had not changed during the experiment, or at any rate that any change in permeability that had occurred did not affect the readings taken. No serious attempt was made to determine the completeness of semipermeability. Preliminary experiments indicated that the membranes were slightly permeable to sodium chloride, but a passage of cane sugar through the membrane was not detected. Conductivity measurements are to be made to determine the permeability of these membranes to salts, and these results will be reported in a later paper.

Preparation of solutions.—Cane sugar solutions were prepared in accordance with tables given by FINDLAY (**11**), rock candy being used. Sodium chloride was made up on the volume molecular basis and its osmotic pressure figured from the data given by RENNER (**25**).

Capillary tube errors.—Although according to the law of POISEUILLE the flow of water through capillary tubes is affected by temperature, it is not believed that this was a factor in these experiments. In POISEUILLE'S experiments the liquid was subjected to a head of pressure and flowed through the capillary tube with rapidity, whereas in these experiments there was no hydrostatic pressure applied and the rate of movement through the tube was very slow. According to BARKER (**3**), when water is the liquid in question this law applies only to tubes with less than 0.5 mm. diameter of capillary; while the capillary used in these experiments was 1 mm. It is not believed that the results obtained are affected by the influence of temperature on the flow of water through the capillary tube of the apparatus.

Other precautions taken.—All membranes were heated in boiling water before being used for experimental purposes. The distilled water used inside the osmometer was previously boiled to drive off dissolved gases. Tests were made to determine that no leakage was occurring in the apparatus. In filling the osmometer care was taken to drive out all air bubbles from the internal portion of the apparatus. Special pains were taken to see that no air bubbles were lodged on the membrane.

Effect of temperature

Membranes of the seed of *Arachis hypogaea* were placed in the osmometer and measurements were made of the rate of penetration of water at the temperatures indicated. After being measured at the various temperatures, each membrane was checked back

TABLE II

EFFECT OF TEMPERATURE UPON PERMEABILITY OF SEED COAT (MEMBRANES OF *Arachis hypogaea*)

Number	Osmotic pressure at 25°C.	Water (in mg.) passing through 19.635 sq. mm. of membrane per hour				
		5°.2 C	15°.2 C	25°.2 C	35°.0 C	45°.0 C
1	27.65	11.01	18.59	29.09	.....	.....
2	"	22.93	38.08	58.19	.....	.....
3	"	.....	.....	56.48	78.71	104.85
4	"	.....	.....	68.46	91.18	126.78
5	41.48	16.51	28.32	42.70	.....	.....
6	"	33.02	53.12	82.15	.....	.....
7	"	42.19	69.07	102.60	128.69	161.83
8	"	37.91	59.03	88.99	106.87	142.83
9	13.82	.....	.....	28.52	40.59	52.96
10	"	.....	.....	35.37	50.82	71.68
11	"	13.45	21.25	34.23	47.22	61.09
12	"	15.41	24.79	35.94	46.40	64.20

From left to right, the figures are readings obtained from the same individual membrane at different temperatures; each line represents a different membrane.

against a previous temperature to be certain of constant behavior. In transferring from one temperature to another the membrane was not removed from the osmometer, so that the results indicated in table II show a comparison of the rates indicated by the same membrane at different temperatures. When the bathing solution was changed from one temperature to another its osmotic pressure also changed, and a correction was made for this change in osmotic

pressure of the bathing solution due to changes in temperature. The actual osmotic pressure of the solution at the temperature used was calculated on the basis of proportionality between osmotic pressure and absolute temperature. The observed rate was corrected on the basis that the rate was proportional to the pull applied, which will be shown later to be the case for solutions of sodium chloride. When cane sugar was used as the bathing solution the observed rate was not corrected, because proportionality between rate and pull applied does not exist with such solutions.

TABLE III

VALUE OF Q_{10}

5.2–15.2° C.	15.2–25.2° C.	25.2–35.0° C.	35.0–45.0° C.
1.688	1.564	1.374	1.332
1.661	1.528	1.339	1.300
1.716	1.512	1.258	1.250
1.609	1.546	1.206	1.364
1.637	1.487	1.433	1.305
1.530	1.507	1.448	1.411
1.579	1.610	1.388	1.294
1.608	1.449	1.298	1.384
Average, 1.628	1.525	1.343	1.344

TABLE IV

EFFECT OF TEMPERATURE UPON PERMEABILITY OF SEED COAT (MEMBRANES OF *Arachis hypogaea*)

Number	Osmotic pressure of cane sugar solution at 25° C.	Water (in mg.) passing through 19.635 sq. mm. of membrane per hour			
		3.6° C	13.6° C	23.6° C	33.6° C
1	21.25	7.98	13.69	20.54	26.81
2	"	13.12	21.11	30.07	42.21
3	"	11.64	19.40	28.92	38.79
4	"	6.39	10.27	14.38	19.51
5	"	14.55	23.39	35.09	46.89

From table II we may estimate the coefficients for 10° rise in temperature (see table III), hereafter referred to as Q_{10}. Experiments were carried out also in which cane sugar was used as the bathing medium instead of sodium chloride. The results with cane sugar are given in table IV. The figures in table IV give

coefficients for 10° C. as recorded in table V. These data were not corrected for change in osmotic pressure due to change in temperature, because, as will be shown later, the rate is not exactly proportional to the pull applied. But that this correction would

TABLE V

VALUE OF Q_{10}

3.6–13.6° C.	13.6–23.6° C.	23.6–33.6° C.
1.716	1.541	1.305
1.610	1.424	1.403
1.667	1.492	1.342
1.607	1.400	1.357
1.607	1.500	1.336
Average, 1.641	1.463	1.348

be a small one and that it would not affect the general results, is indicated by the following results obtained when a correction is figured on the assumption that the rate is proportional to the pull. Making this correction, the first column of table IV, showing values of Q_{10}, becomes:

1.640
1.547
1.604
1.545
1.546

Average, 1.578

In addition to this, preliminary results were obtained from measurements of 6 other membranes. While the conditions of the experiment were not so accurately controlled, the average coefficients obtained were as follows:

Approximately 5 to 15° Q_{10} = 1.617
" 15 to 25° Q_{10} = 1.470
" 25 to 35° Q_{10} = 1.422

Temperature coefficients.—The effect of temperature upon a process has been much used to obtain information as to its nature, that is, whether chemical or physical. Generally speaking, chemical processes follow the van't Hoff law (Q_{10} = 2 to 3), but the effect of

temperature upon the process of diffusion is such that Q_{10} is approximately 1.3. Applying the results of these experiments to this case it is found that the coefficient obtained does not correspond with either the van't Hoff coefficient or the diffusion coefficient. Measurements of the permeability of membranes made heretofore have shown in general a temperature coefficient approximating that of the van't Hoff law, but there is no evidence in these experiments that in the passage of water through the seed coat of the peanut chemical processes are exclusively involved. Apparently also the effect of temperature is not merely upon the rate of diffusion of water. Probably we are not justified in using the numerical coefficients obtained to form any conclusion as to the nature of the process by which water passes through the peanut membrane.

Comparison with temperature coefficients obtained by others.—KRABBE (**19**) measured the effect of temperature upon the permeability of the living cells of cylinders of pith of *Helianthus annuus* and pieces of roots of *Vicia Faba*, etc. As criteria he took the rate of increase in length of pieces of plasmolysed tissue, allowed to absorb water at temperatures in vicinity of 0° and 20° C, and the length of time for plasmolysis to occur at these temperatures. He found that the velocity of water movement increased 3–5 times when the temperature was increased 20° C. (Q_{10} approximately 2.0–2.5). He believed that this high coefficient indicated that purely physical forces were not operative, but that it was due to a specific property of living protoplasm.

RYSSELBERGHE (**26**) investigated the effect of temperature upon the permeability of the living protoplasm, using pith cells of *Sambucus nigra*, lower epidermal cells of *Tradescantia*, and filaments of *Spirogyra*. He made use of 3 methods: the rate of shortening of a tissue in a plasmolysing solution at different temperatures, the rate of elongation of plasmolysed tissue in water at different temperatures, and the rate of plasmolysis of a tissue under microscopic observation. His general results are as follows:

Temperature	0	6	12	16	20	25	30
Comparative rate	1	2	4.5	6	7	7.5	8

This gives an average value for Q_{10} from 0°–30° of 2.0. RYSSELBERGHE does not agree with KRABBE that this high coefficient necessarily indicated the special activity of vital matter.

BROWN and WORLEY (6) determined the speed of intake of water by barley grains immersed in water at different temperatures. Their results gave a temperature coefficient of 1.8–1.9. Since this approached closely the van't Hoff coefficient (2–3) for the effect of temperature on the rate of chemical reaction, they considered that chemical processes were involved in the penetration of water through the semipermeable membrane of the barley grain. This chemical reaction, according to their view, took place in the water itself, that the effect of temperature was to split the larger aggregates of water into simpler ones, and that only these simpler molecules were transmitted by the differential septum. This was offered as evidence in favor of the hydrone conception of ARMSTRONG (1) as to the composition of water.

PFEFFER (24) measured the rate of water movement across the copper ferrocyanide membrane at different temperatures with the following results:

Temperature	In stream per hour
7°.1	5.9 mm.
17°.6	9.4 "
32°.5	13.3 "

The above figures give values of Q_{10} as follows:

$$7.1\text{–}17°.6,\ Q_{10}=1.558$$
$$17.6\text{–}32°.5,\ Q_{10}=1.266$$

The writer's observed values are in fair agreement with these figures. For purposes of comparison, a summary is given in table VI. It will be noted from this table that no parallel exists between

TABLE VI

Observer	Nature of membrane studied	Temperature range	Q_{10}
Krabbe	Living pith cells of *Helianthus*	0–4 to 20–26°	2.0 to 2.5
Rysselberghe	Living cells	0 to 30°	2.0
Brown and Worley	Semipermeable membrane of barley seed	3.8 to 34°.6	1.9 to 1.8
Pfeffer	Copper ferrocyanide	7.1 to 32°.5	1.558 to 1.266
The writer	Seed coat of *Arachis hypogaea*	3.6 to 45°	1.641 to 1.343

the nature of the membrane studied and the value of the coefficient observed. If this were the case, the barley and peanut membranes

should be expected to give similar results, while the similarity of results given by the copper ferrocyanide membrane and peanut should not be expected. We may note, however, a parallel between the method of observation employed and the coefficient obtained. The first 3 observers studied the permeability of the membrane indirectly, other structures such as cell contents and seed contents being present. In the last two cases the membrane was measured directly, without other structures being factors in the rates observed.

It is questionable to what extent results obtained by the indirect method may be referred to the membrane alone. There is the possibility that the temperature effect may have been, not upon the membrane merely, or upon the water exclusively, but also upon the cell contents or seed contents. The latter effect may have contributed to the total results from which the coefficients were calculated. The chemical reaction indicated by the coefficient 2–3 may have taken place in that phase of the system that was internal to the membrane studied.

In these experiments the temperature may have exerted an effect on the water, but if so the temperature coefficient does not indicate that this was related to a chemical reaction. There is no evidence of a temperature action in splitting the larger water aggregates into simpler hydrone molecules as found by BROWN and WORLEY with the semipermeable membrane of the barley grain.

Tendency of temperature coefficients to fall in value with increased temperatures.—An inspection of the temperature coefficients obtained in these experiments shows that the coefficients are higher at the lower temperatures and lower at the higher temperatures. This has been found to hold for a great many different processes. KANITZ (**18**) noted a number of physiological processes that show this tendency. SNYDER (**29**) has pointed out that some purely chemical reactions also exhibit a falling value of Q_{10}, and COHEN-STUART (**8**) has shown that according to the van't Hoff law itself values of Q_{10} are not constants and that the velocity is not an exponential function of the temperature. Table VII indicates the general tendency of Q_{10} for different processes. Falling values of Q_{10} are thus shown to occur in measurements made (*a*) with living matter, (*b*) with non-living matter, (*c*) with a physical

process, and (*d*) with a chemical process. These figures also emphasize the fact that temperature coefficients should not be averaged for a large interval of temperature, but that the range of the values of Q_{10} for each temperature interval should be shown for which experimental data are available.

TABLE VII

RYSSELBERGHE'S RESULTS WITH LIVING PROTOPLASM		RESULTS OBTAINED WITH NON-LIVING PLANT MEMBRANES		VAPOR PRESSURE OF WATER AT VARIOUS TEMPERATURES		REMSEN AND REID'S RESULTS WITH HYDROLYSIS OF NITRO-BENZAMIDE*	
Temperature	Q_{10}	Temperature	Q_{10}	Temperature	Q_{10}	Temperature	Q_{10}
0–6°	3.2	5.2–15.2	1.628	5–15°	1.043	60–70°	1.84
6–12	3.8	15.2–25.2	1.525	15–25	1.854	70–80	1.72
12–16	2.0	25.2–35.0	1.343	25–35	1.776	80–90	1.65
16–20	1.5	35.0–45.0	1.344	40–50	1.675	90–100	1.59
20–25	1.1	.....	.....	.....	.....	.....	.....
25–30	1.1	.....	.....	.....	.....	.....	.....

* From data given by SNYDER (**29**, p. 169).

Relations of permeability of membranes to vapor pressure of water.—The experiments of BROWN and WORLEY (**6**) showed that Q_{10} approximated in numerical value the vapor pressure coefficients of water at those temperatures. From table VII it will be noted that similar results were not obtained with the peanut membrane; that while the coefficient of permeability rates and vapor pressure are not equal, they both show the same tendency to fall in value at higher temperatures. It may be noted in this connection that the coefficient obtained lies between the diffusion coefficient and the vapor pressure coefficient.

Rate as related to flow through capillary tubes.—According to the law of POISEUILLE, as reported by KRABBE (**19**), the quantity of water flowing through a glass tube increases from 1 to $1+0.0336793\ t+0.000220936\ t^2$, where t is the temperature in degrees Centigrade (KRABBE **19**, p. 477). This would make the coefficient for 10 rise in temperature about 1.358. Since this law applies only to capillary tubes with a length above a certain minimum amount, and since the temperature coefficients obtained in these experiments are not constants but vary with the temperature, it is not believed

that the results obtained indicate that the passage of water through the membrane is analogous to the passage of water through capillary tubes.

Rate as related to previous heating or cooling.—When the permeability of a membrane is measured at one temperature and the membrane then transferred to another temperature, the question is raised as to whether or not there is any "after effect" of the previous temperature. To determine this point membranes were fitted into 2 osmometers and a measurement was made of the permeability of each membrane. One osmometer was then placed in a beaker of water in an ice chest at 2.5 C., and the other in an oven at 46° C. The next day the two were again placed in the original osmotic solution at the original temperature and readings again taken. The results obtained are given in table VIII. No after effect of a previous temperature, or hysteresis, was observed at the temperatures used in these experiments.

TABLE VIII

Intervals of 10 minutes	25° C.	25° C.
First membrane		
First	27 spaces	29 spaces*
Second	29 "	29 "
Third	28 "	29 "
Fourth	29 "	29 "
Fifth		29 "
Second membrane		
First	23 spaces	23 spaces†
Second	23 "	24 "
Third	23 "	24 "
Fourth	24 "	22 "
Fifth		23 "

* After 14 hours at 2.5° C.
† After 15 hours at 45° C.

Rate as affected by direction of flow of water through membranes.—A peanut seed coat membrane was placed in an osmometer and a measurement made of the rate at which water passed through it. The membrane was then removed from the osmometer and its position reversed, the opposite surface being turned toward the

inside of the osmometer. The latter was then placed again in the original solution and a reading made of its rate of water passage. Table IX indicates the results obtained. The peanut membrane therefore is more permeable for water in one direction than in the other, and the favorable direction is from the outside toward the inside.

TABLE IX

RATE AS AFFECTED BY DIRECTION OF FLOW OF WATER THROUGH MEMBRANE OF *Arachis hypogaea*

NUMBER	DIAMETER OF HOLE	OSMOTIC PRESSURE	WATER (IN MG.) PASSING THROUGH MEMBRANE PER HOUR				
			In	Out	In	Out	Percentage decrease from in to out
1	8 mm.	67	139.52	95.92	135.16	90.91	32
2	"	"	137.34	87.20	111.18	84.58	31
3	"	"	124.26	93.09	.....	.....	25
4	"	"	99.25	43.21	98.86	.....	56
5	"	100	396.21	207.04	402.67	205.07	49
6	"	"	236.88	158.20	224.80	146.12	34
7	"	"	164.38	121.27	202.32	137.59	32
8	5 "	25	36.80	20.82	30.04	24.70	32
9	"	"	30.55	27.70	38.02	26.98	20
10	"	48	.....	70.17	106.11	.....	33
11	"	"	.....	79.87	111.82	.....	38
12	"	"	.....	35.05	53.77	.....	33
13	"	"	.....	44.75	63.69	44.50	20
14	"	"	.....	49.06	71.88	.....	31

"In" means direction outside of seed toward inside; "out" means direction inside of seed toward outside.

Measurements with the seed coats of *Prunus Amygdalus dulcis* gave the following results:

Rate in = 48.5 mg. per hour
Rate out = 42.6 " " "
Rate in = 48.5 " " "
Rate out = 40.4 " " "

Measurements made with the onion scale and with the seed coat of *Dioon edule* did not indicate any observable difference in the rate of penetration in opposite directions. This difference in the behavior of the two types of membranes may be correlated with their differences in structure. The peanut and almond seed coats are composed of two or more distinct layers, and have surfaces of different physical and chemical nature on opposite sides; such is

not the case with onion and cycad membranes. The differences in rate in opposite directions through a membrane have long been known to workers with animal membranes. MATTEUCCI and CIMA (**21**) in 1845 observed it with the skin of the frog and eel. COHNHEIM (**9**), according to HAMBURGER, ascribed the same phenomenon to the living action of the intestinal membrane. HAMBURGER (**14**) showed that this behavior was not restricted to living membranes, but that non-living animal membranes gave similar results; in fact, he prepared artificial membranes from parchment with layers of collodion, chromgelatin, and chromalbumen that were more permeable in one direction than in the other. He ascribes this to the "double" nature of the membrane, and the writer's results offer evidence in favor of HAMBURGER'S interpretation. If this difference in rate is due to the presence of double membranes of different nature, or to differences in surface on opposite sides, may not the plant cell itself show a difference in permeability in opposite directions, since such a system of double membranes is represented by the cell wall and ectoplast?

Rate as related to the concentration of the external solution.— Solutions of different osmotic pressures were used as the external solution in order to determine whether or not the rate of water

TABLE X

RELATION BETWEEN OSMOTIC PRESSURE APPLIED AND RATE (SODIUM CHLORIDE SOLUTION)

Number	Water (in mg.) passing through membrane per hour in atmospheres of osmotic pressure		
	13.82	27.65	41.48
1	22.53	44.37	67.89
2	21.96	44.37	66.75
3	.....	28.09	42.79
4	.....	58.18	82.15
5	28.53	56.48	.....
6	35.37	68.93	.....
7	34.23	.....	102.69
8	35.94	88.0	88.99

movement was proportional to the pull applied. Two solutions were used, sodium chloride and cane sugar. The results with sodium chloride are shown in table X. A comparison of the

osmotic pressure and rates from the data in table X is given in table XI.

TABLE XI

Ratio of pressures 27.65:13.82	Ratio of rates	Ratio of pressures 41.48:27.45	Ratio of rates	Ratio of pressures 41.48:13.84	Ratio of rates
2.000.....	1.969	1.500.....	1.530	3.000.....	3.013
2.000.....	2.020	1.500.....	1.504	3.000.....	3.040
2.000.....	1.980	1.500.....	1.471	3.000.....	3.029
2.000.....	1.949	1.500.....	1.412	3.000.....	2.977

TABLE XII

RELATION BETWEEN OSMOTIC PRESSURE APPLIED AND RATE (CANE SUGAR SOLUTION)

Number	Water (in mg.) passing through membrane in atmospheres of osmotic pressure					
	5.15	10.30	15.62	21.25	29.22	48.00
1.....	.....	23.39	29.44	33.66	.....	.....
2.....	.....	29.44	37.65	.....	.....	.....
3.....	9.70	21.11	27.09	35.37	.....	.....
4.....	8.55	18.25	24.53	31.95	.....	.....
5.....	8.16	16.83	24.25	28.43	.....	.....
6.....	7.70	13.35	18.17	21.96	.....	.....
7.....	14.09	27.04	36.62	45.18	.....	.....
8.....	14.73	25.84	35.26	42.79	.....	.....
9.....	11.81	19.40	23.96	28.24	.....	.....
10.....	12.83	23.45	31.66	35.37	.....	.....
11.....	10.84	21.11	27.95	33.66	.....	.....
12.....	13.09	24.53	31.95	39.36	.....	.....
13.....	5.53	9.09	11.98	13.09	.....	.....
14.....	6.84	11.72	13.09	16.54	.....	.....
15.....	11.98	23.96	29.66	36.97	.....	.....
16.....	.....	23.10	28.07	34.80	.....	.....
17.....	.....	.....	.....	.....	41.07	53.05
18.....	.....	.....	.....	.....	50.49	63.32
19.....	.....	.....	.....	.....	64.75	84.72

A comparison of the ratios of pressure and the ratios of the rates indicated in table XII is given in table XIII.

When the ratios of pressure applied were 2.000, 1.515, 1.360, and 1.642, the average ratio of rates observed was 1.888, 1.297, 1.211, and 1.285 respectively. It will be seen that the rate of water penetration is nearly proportional to the pull applied when sodium chloride is used, but that when cane sugar is used as the external solution, the rate is not proportional to the pull, but the

coefficient falls off with the higher concentrations. It is believed that this lowering of the rate is due to the increasing viscosity of more concentrated sugar solutions.

TABLE XIII

RATIOS OF RATES

5.15:10.30	10.30:15.62	15.62:21.25	29.22:48.0
2.176	1.259	1.144	1.292
2.133	1.279	1.305	1.254
2.063	1.284	1.302	1.308
1.734	1.344	1.172	.....
1.919	1.441	1.209	.....
1.756	1.361	1.234	.....
1.634	1.354	1.214	.....
1.825	1.304	1.179	.....
1.947	1.235	1.117	.....
1.792	1.351	1.204	.....
1.753	1.325	1.233	.....
1.712	1.302	1.143	.....
2.000	1.235	1.208	.....
"	1.168	1.246	.....
"	1.238	1.249	.....
"	1.215	1	.....
Average, 1.888	1.297	1.211	1.285

It was found that it was not possible to increase the concentration of the solutions on opposite sides of a membrane by an equal amount on each side without changing the rate at which water passed through the membrane. This was done in the following way: distilled water was placed inside the osmometer, the apparatus surrounded by a solution of sodium chloride having a known osmotic pressure, and the rate of water movement measured. Then the osmotic pressure was increased on each side of the membrane by an equal amount. The results are given in table XIII. Thus, although the effective osmotic pressure exerting an influence upon water movement was practically the same, the rate of water movement was not the same, but much less. With the same membrane the same osmotic pull does not give the same rate, but the rate depends upon the distribution of the concentration on opposite sides of the membrane. When the concentration of the external solution was kept constant and the concentration of the internal solution was varied, the results given in table XIV

were obtained with sodium chloride solutions. From these data the writer has not been able to formulate any mathematical relation between differences in concentration on opposite sides of the membrane and the rate of water movement through it. Another

TABLE XIII

RATE OF WATER MOVEMENT AS RELATED TO DIFFERENCES IN CONCENTRATION OF SOLUTIONS ON OPPOSITE SIDES OF MEMBRANE

Membrane	Solution	Osmotic pressure of external solution	Osmotic pressure of internal solution	Effective osmotic pressure	Rate per hour
First	Na Cl	18.43	0	18.43	48.29
"	"	36.86	18.43	18.43	35.94
Second	"	13.82	0	13.82	41.07
"	"	27.65	13.82	13.83	23.96
Third	Sugar	10.30	0	10.30	20.54
"	"	21.25	10.30	10.95	10.84
Fourth	"	10.30	0	10.30	29.09
"	"	21.25	10.30	10.95	15.63

TABLE XIV

FALL IN RATE OF WATER MOVEMENT WHEN CONCENTRATION OF INTERNAL SOLUTION WAS INCREASED

OSMOTIC PRESSURE OF EXTERNAL SOLUTION	OSMOTIC PRESSURE OF INTERNAL SOLUTION	WATER (IN MG.) PASSING THROUGH MEMBRANE PER HOUR	
		First	Second
46.10	0	67.74	61.67
"	4.61	49.54	45.21
"	9.22	45.49	39.43
"	13.82	39.39	32.99
"	18.43	26.96	24.27
"	23.05	22.92	18.86
"	27.65	12.13	10.11

set of readings was taken in which cane sugar solutions were used. The results are given in table XV, and show that the relation between concentration and rate is complex.

From the data given in tables XIII–XV we may conclude: (1) that the rate is greatly affected by changes in the concentration of the internal solution; (2) that equal osmotic differences do not necessarily produce equal rates; and (3) that no mathematical relation has been noted between the concentration on opposite

sides and the rate of water movement through the membrane. This emphasizes the caution that must be used in plasmolytic experiments on the rate of water movement through a membrane. Plasmolysis deals with solutions of different concentrations on opposite sides of a membrane. The concentration of only one of the solutions, the plasmolysing solution, is known. In such experiments the internal concentration of the cells of plant or seed is not known and is subject to change, that is, to variations in pulling power. Results should not be referred to changes in the permeability of the membrane alone until it has been found that the internal concentration has remained constant during the experiment (it is to be understood that this statement is intended to apply to *rate of water movement* and not to the final equilibrium attained by the two solutions).

TABLE XV

RATE OF WATER MOVEMENT AS RELATED TO DIFFERENCES IN CONCENTRATION OF SOLUTIONS ON OPPOSITE SIDES OF MEMBRANE

OSMOTIC PRESSURE OF EXTERNAL SOLUTION	OSMOTIC PRESSURE OF INTERNAL SOLUTION	EFFECTIVE OSMOTIC PRESSURE	WATER (IN MG.) PASSING THROUGH MEMBRANE PER HOUR	
			First	Second
73.69.....	0	73.69	41.07	37.65
48.0.....	0	48.0	37.65	34.23
21.25.....	0	21.25	27.38	21.39
10.30.....	0	10.30	13.59	17.11
73.69.....	10.30	63.39	21.39	20.54
73.69.....	21.25	52.42	9.58	11.13
48.0.....	10.30	37.70	17.11	16.26
21.25.....	10.30	10.95	6.84	8.56

Comparison of permeability of membranes of different species

Membranes from different species showed large differences in permeability, as indicated by table XVI. Equal areas (19.635 sq. mm.) of membranes were measured; saturated sodium chloride of approximately 375 atmospheres osmotic pressure was used as the external solution. It will be seen that membranes of different species and different membranes of the same species show large differences in permeability. The causes of these differences in the

rate of penetration will be dealt with in a later paper. It may be stated here, however, that thickness of membrane is not the limiting factor. The thinnest membrane is that of *Cucurbita*, and the thickest is that of *Prunus Amygdalus*.

TABLE XVI

RELATIVE PERMEABILITY OF VARIOUS MEMBRANES

Membrane	Water (in mg.) passing through per hour	Membrane	Water (in mg.) passing through per hour
Citrus grandis	0	Allium Cepa	39.2
" "	0	" "	12.9
" "	0	" "	12.3
" "	0	" "	31.2
Cucurbita Pepo	7.3	" "	22.4
" "	4.8	Prunus Amygdalus dulcis	120.0
" "	0	" " "	144.0
" "	4.0	" " "	72.0
" maxima	11.0	" " "	86.0
" "	0	" " "	60.0
" "	9.0	" " "	72.0
" "	11.3	" " "	72.0
" "	15.3	Arachis hypogaea	328.0
Xanthium pennsylvanicum	20.0	" "	530.0
" "	16.0	" "	564.0
" "	14.7	" "	710.0
" "	22.0	" "	528.0
Juglans regia	32.0	" "	672.0
" "	22.7	" "	584.0
Allium Cepa	25.7	Dioon edule	777.5

Structures of membrane used

The layers of tissue represented in the ripened seed coat of the various species and their origin have not been accurately determined by an examination of successive stages of the development of the seed. A study of the histology of the seeds of *Cucurbita* has been made by BARBER (**2**), of *Prunus Amygdalus* by PÉCHOUTRE (**23**), of *Xanthium* by HANAUSEK (**15**), of the Leguminosae by PAMMEL (**22**), and of the seed coats of various species in many families by LONAY (**20**), BRANDZA (**7**), GUIGNARD (**12**), and HARZ (**17**). From an examination of sections of the membranes used, and from a comparison made with the reports of these investigators, it is believed that the following structures are involved in these membranes: (1) an outer integument, a much compressed and hardly

distinguishable inner integument and nucellus, and a single layer of endosperm in *Arachis hypogaea* and *Prunus Amygdalus dulcis;* (2) a single integument and a layer of endosperm in *Xanthium pennsylvanicum* and *Juglans regia;* and (3) a portion of the integument, a layer of perisperm, and a layer of endosperm in *Cucurbita Pepo* and *C. maxima.* Details of the structure of these membranes, and a microchemical and chemical study of their composition will be given in a later paper.

Summary

1. Quantitative measurements were made of the permeability to water of certain non-living semipermeable plant membranes under experimentally controlled conditions.

2. The apparatus and method employed had the following advantages over osmometers ordinarily employed: (1) the passage of as small a quantity of water as 0.000337 gm. could be detected; (2) the exact area of the membrane used could be calculated; (3) the concentration of the solution exerting the osmotic pressure could be kept constant.

3. The effect of temperature upon the permeability to water of the seed coat of *Arachis hypogaea* was measured and the temperature coefficients for 10° rise in temperature were obtained. An average coefficient was not calculated. Since the temperature coefficients are not constant, but vary with the temperature, an average coefficient is without significance.

4. The temperature coefficient is lower than that according to the van't Hoff law, and is higher than the diffusion coefficient. There is no evidence that either chemical or physical processes are exclusively involved in the passage of water through the membrane.

5. The temperature coefficients showed higher values at lower temperatures and lower values at higher temperatures, and this is in agreement with the behavior of temperature coefficients in other processes.

6. A comparison is made with the temperature coefficients obtained in the permeability experiments of (1) KRABBE with living membranes, (2) RYSSELBERGHE with living membranes, (3)

BROWN and WORLEY with non-living seed coat membranes, (4) PFEFFER with copper ferrocyanide membrane.

7. No hysteresis or after effect of a previous temperature was observed.

8. It was found that the seed coats of peanut and almond showed a difference in permeability to water in opposite directions through the membrane, the faster rate being from the external toward the internal portion of the seed.

9. When distilled water was placed on one side of the membrane, the rate of water movement was proportional to the osmotic pressure applied upon the other side, when sodium chloride solutions were used; but this proportionality did not exist when cane sugar solutions were used.

10. When solutions of varying concentrations were placed on opposite sides of the membrane, it was found that the relation between rate and concentration difference was complex, and that in general equal osmotic differences do not necessarily produce equal rates; the rate is greatly affected by changes in the concentration of the internal solution; no mathematical relation was noted between the concentration on opposite sides and the rate of water movement through the membrane. The bearing of these facts upon plasmolytic experiments based on rate of water movement through membranes was pointed out.

11. A comparison of the permeability of several plant membranes under similar conditions was made, large differences appearing.

In conclusion, I wish to express my appreciation to Dr. WILLIAM CROCKER for suggesting the problem and rendering valuable assistance during the course of the experiments.

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ARBORES FRUTICESQUE CHINENSES NOVI. I

CAMILLO SCHNEIDER

Deutzia (Sect. EUDEUTZIA, subsect. STENOSEPALAE Schn.) **Rehderiana,** sp.n.—Frutex ut videtur mediocris, dense breviter ramosus; ramuli annotini biennesque dense scabriter stellato-pilosi, rubro-fusci, vetustiores glabrescentes, cortice detersili; gemmae parvae, perulis pluribus lanceolatis acuminatis fusco-rubris pilosis cinctae. Folia matura papyracea, ovato-oblonga vel pleraque satis late ovata, apice satis sensim acuta, basi rotundata, margine breviter et subdistanter argute serrata, 1.5–2.5 cm. longa, 0.8–2 cm. lata vel surculorum ad 3.8:2.5 cm. magna, superne obscure viridia, scabra, pilis stellatis (4–)5–7 (–8)-radiatis subdense vel sparsius conspersa, subtus pallidiora, subcinerascentia vel in sicco interdum quasi caesio-viridia, in facie pleraque densius in nervis laxius pilosa pilis 5–7–9 radiatis, nervis lateralibus utrinsecus 4–5; petioli 1–3 mm. longi, superne sulcati, undique dense stellato-pilosi. Cyma 3–8-flora, pleraque subsessilis, ramulos laterales breves 1–2 rarius ad 4 cm. longos terminans, plus minusve dense stellatopilosa; pedicelli graciles, fructiferi ad 5–6 mm. longi; calyx stellatotomentosus pilis homomorphis 9–12-radiatis, dentibus triangulari-lanceolatis tubum aequantibus vel subaequantibus rarius subsuperantibus acuminatis intus glabris; petala alba (vel lactea?), extus sparse stellato-pilosa, ovato-vel elliptico-oblonga, apice satis acuta, 7–9 mm. longa, 3–4 mm. lata; stamina exteriora longiora petalis circ. duplo breviora, interiora exterioribus paullo breviora; filamenta exteriorum apice manifeste bidentata dentibus latis rectangularibus vel subtriangularibus antheram breviter stipitatam subaequantibus vel parum superantibus interdum anthera brevioribus, interiorum lata, apice truncata et irregulariter denticulata vel versus apicem sensim acuta, antheram faciei interiori circa medium affixam gerentia; styli 3 laciniis calycis vix longiores. Capsula hemisphaerica, circ. 3 mm. crassa, lobis erectis vel incurvis plus minusve deciduis.

Yunnan occidentalis: inter Talifu et Tengyüeh, probabiliter in regione inter flumina Mekong et Salween, Octobri 1914, *C. Schneider* (no. 2613; typus in Herb. Arb. Arn. et in Hb. Schneider).

This is a very distinct looking plant, with its small, broadly ovate, almost subsessile leaves, and its few-flowered inflorescences which are borne on short lateral branchlets. It seems to be most closely related to *D. subsessilis* Rehd., which may easily be distinguished by its much longer (up to 6 cm.), more oblong leaves whose stellate hairs of the under surface have only 4–6 rays, by its larger and richer inflorescences, and by its larger flowers.

It is with great pleasure that I connect with this distinct species the name of Mr. ALFRED REHDER, the well known dendrologist of the Arnold Arboretum, who (SARGENT, Pl. Wils. 1:1913) has given an excellent contribution to the knowledge of the genus *Deutzia*.

Spiraea (Sect. CHAMAEDRYON Ser.) **teretiuscula,** sp.n.—Frutex latus, ad 2 m. altus, laxe ramosus, ramis subnutantibus; ramuli hornotini flavescentes vel violascentes, vix sulcato-striati, puberuli, annotini rubro-brunnei vel fusci, teretiusculi, vetustiores cinerascentes; gemmae ut videtur parvae, ovatae, perulis imbricatis pilosis obtectae. Folia decidua, ovalia, obovalia vel ovato-elliptica, apice rotundata, interdum fere subemarginata, minutissime apiculata, basi plus minusve late cuneata, 6–11 mm. longa, 3–7 mm. lata, margine integerrima, superne laete viridia, tantum novella minutissime puberula, cito glaberrima, subtus discoloria, cinerascentia, initio paullo distinctius pilosa, dein etiam glabra, sub microscopio ut in *S. canescenti* papillosa, nervis utrinsecus 3–4 vix visibilibus; petioli flavescentes, vix 1.5 mm. longi, puberuli. Corymbus circ. 25-florus, convexus, tomentosulus, ramulos normaliter plurifoliatos 1–3 cm. longos terminans, 1.5–2.5 cm. diametiens; flores albi, circ. 5 mm. diametientes; pedicelli graciles, floribus breviores, tomentosuli; receptacula late turbinata, extus tomentosula, intus pilosula; sepala late triangularia, receptaculis aequilonga, extus glabra, intus ad apicem et ad marginem fulvo-villosula; petala suborbicularia, circ. 1.5 mm. lata, sepala duplo superantia; stamina 20, petalis subaequilonga; discus distinctus 10-lobatus, lobis apice dorsoque leviter sulcatis; carpidia extus versus basim intus ad ventrem sparse villosa, stylis apicalibus quam stamina subduplo brevioribus. Fructus maturi ignoti.

Szechuan australis: in regione Yen-yüan Hsien, inter viculos Ka-la-pa et Liu-ku, in dumetis montanis, alt. circ. 3000 m., 17 Maji 1914, *C. Schneider*

(no. 1256); eadem regione, prope Kua-pie, in declivibus calcareis montium, alt. circ. 3000 m., 23 Maji 1914, *C. Schneider* (no. 3546; typus in Herb. Arb. Arn. et Hb. Schneider).

At first sight, this species seems to be much like *S. ovalis* Rehd., which also has terete branchlets and similar leaves and flowers, but which is easily distinguished by the glabrous branchlets, leaves, and inflorescence, as well as by the leaves being not papillose beneath. According to the papillose leaves, *S. teretiuscula* is more closely related to *S. canescens* Don, but all the forms of this variable species have the branchlets distinctly angular.

Here may be mentioned another interesting form I collected in southern Szechuan "in dumetis montium inter viculos Hun-ka et Wo-lo-ho, alt. circ. 3300 m., 13 Junii 1914 (no. 3525; frutex circ. 2 m. altus, alabastra rosea)," the flower buds of which are pink. In its angular branchlets it resembles *S. canescens*, but the young ovate or ovate-elliptic leaves are not distinctly papillose beneath. Judging by its pinkish flowers it seems to represent a new species, but, unfortunately, the flowers are too young to furnish sufficient characters for a description. The young branchlets, leaves, and inflorescences are not quite so distinctly puberulous as in *S. teretiuscula*, and they seem to become very soon almost glabrous. The leaves are entire, and measure up to 15 mm. in length and 7 mm. in width.

MALUS PUMILA Mill., var. **subsessilis,** n.var.—A typo praecipue recedit fructibus immaturis subsessilibus iis *Docyniae Delavayi* similibus ovato-ellipticis circ. 2.5 cm. longis et 2 cm. crassis sparse villosis apice concavis sepalis persistentibus conniventibus.

Szechuan australis: inter pagos Hoh-si et Te-li-pu, alt. circ. 2300 m., 7 Maji 1914, *C. Schneider* (no. 1132; typus in Herb. Arb. Arn. et Hb. Schneider; tantum arborem unicam mutilatam probabiliter cultam ad 5-metralem vidi).

The subsessile fruit of this apple suggests a *Docynia*, but the leaves and flowers are that of a true *Malus*. So far as I can judge by the material before me, it represents only a form of *M. pumila*, the variability of which needs a careful study. To *M. pumila* sensu meo (Ill. Handb. Laubh. **1**:715. 1905) certainly belongs *M. asiatica* Nakai in Matsumura, Icon. Pl. Koisik. **3**:19. *pl.* 155. 1915.

Malus (Sect. DOCYNIOPSIS Schn.) **docynioides,** sp.n.—Arbuscula squarrosa, ad 6 m. alta; ramuli novelli griseo-villosi, floriferi laxius villosuli ut vetustiores glabrescentes fuscescentes; gemmae satis evolutae ignotae. Folia partim sempervirentia, tenuiter coriacea, biennia elliptico-oblonga vel obovato-elliptica, apice plus minusve rotundata sed apiculata, basim versus sensim attenuata, cuneata, margine subintegerrima vel a medio ad apicem indistincte

glanduloso-crenulata, 2–5.5 cm. longa, 0.7–2 cm. lata vel latiora ad 4.5:2.3 cm. magna, superne intense viridia, nitidula, glabra, subtus pallidiora, laxe villosula, costa nervisque lateralibus utrinsecus plerisque 5 prominulis flavescentibus glabrioribus, petiolis superne sulcatis saepissime laxe villosulis ad 1 cm. longis; folia novella versus apicem pleraque distinctius crenato-dentata vel irregulariter sublobulato-dentata, ad 3:1.7 cm. magna, superne in costa sparse lanuginosa, subtus satis dense griseo-villosula, in costa nervisque tomentella, petiolis ad 8 mm. longis tomentellis. Flores ad 1–3 fasciculati, fere sessiles, albi, circ. 2.5 mm. diametientes; sepala 4–5 mm. longa, late triangularia, subito breviter acuminata, utrinque satis dense lanuginosa, receptaculo dense griseo-villoso-tomentello subaequilonga; petala ovalia, apice rotundata, basi breviter unguiculata, circ. 13 mm. longa et 7 mm. lata; stamina circ. 30, longiora petalis triente breviora, antheris flavis; styli 5, parte inferiore connati, paullo supra basim villosuli, staminibus longioribus breviores; ovarium 5-loculare, loculis in stylorum basi distincte productis 2-ovulatis ovulis plus minusve superimpositis vel appositis. Fructus ignoti.

Szechuan australis: inter Kua-pie et Ta-tiao-ko, alt. circ. 2700 m., 23 Maji 1914, *Schneider* (no. 1349; typus in Herb. Arb. Arn. et Hb. Schneider).

The old leaves of this strange *Malus* are very much like those of *Docynia Delavayi* (Fr.) Schn., which are almost entire but sometimes show a similar dentation. The flowers, however, of *M. docynioides* are different from those of a true *Docynia* in having only 2 ovules in each carpel, while in *D. Delavayi* as well in *D. indica* Decne. I have always found 4–6 ovules. Otherwise the structure of the ovary of our new species agrees with that of the ovary of *M. Tschonoskii* (Max.) Schn. which, as I have pointed out (FEDDE, Rep. spec. nov. 3:179. 1906), may represent the type of a new section for which I proposed the name *Docyniopsis*. The figure given in SARGENT'S *Trees and Shrubs* 1: *pl. 37, fig. 2.* 1903 is incorrect, and has been copied by myself in my *Ill. Handb. Laubh.* 1:*fig. 403h;* the cells of the ovary are distinctly protruding into the base of the styles. As REHDER has stated (SARGENT, l.c. 74), the separation of the genus *Docynia* from *Malus*, especially from the group formerly regarded as genus *Eriolobus*, is rather an artificial one. But, after all, I hesitate to unite the true species of *Docynia* with *Malus*, and I refer to this genus all the species which possess only 2 (very rarely 3) ovules in each cell of the ovary, while *Docynia* may be distinguished by its 4–6-ovulate carpels.

Sorbus (Sect. ARIA) **Ambrozyana,** sp.n.—Frutex elatus vel arbor parva, habitu *S. Ariae;* ramuli annotini glabri, fusco-purpurei,

lenticellis flavis sparse obtecti, vetustiores fusco-nigrescentes; gemmae ovato-oblongae, acuminatae, perulis paucis fusco-purpureis margine dense longiciliatis cinctae, divaricatae, laterales 7–8 mm., terminales circ. 10 mm. (vel ultra?) longae. Folia decidua, subchartacea, pleraque elliptico-oblonga, minora interdum ovato-elliptica et maxima obovato-oblonga, apice acuta vel plus minusve rarius distincte acuminata, basi satis acute vel late cuneata, rarius subrotundata, minora latiora 6–7 cm. longa et 2.5–3.5 cm. lata, oblonga majora 7:2.5 ad 15:4 cm. vel latiora ad 14:6 cm. magna, margine irregulariter vel dupliciter subglanduloso-denticulata vel sublobata, superne saturate viridia, paullo nitidula, glabra (vel juniora ut videtur in costa nervisque subimpressis sparse pilosa), subtus valde discoloria, pulchre albescentia vel leviter flavescentia, facie tomento lanuginoso adpresso obtecta, costa nervisque lateralibus utrinsecus 9–10 subrectis in dentes exeuntibus angulo circ. 45° a costa divergentibus prominentibus sparsius lanuginosis vel fere glabrescentibus colore flavescente conspicuis; petioli 1–2 cm. longi, flavescentes, superne canaliculati, sparse lanuginosi vel fere glabri. Inflorescentia valde deflorata vel fructifera ramos laterales normaliter 2–3-foliatos ad 3 cm. longos terminans, corymbosa, circ. 5 cm. longa et lata, sparse pilosa vel glabra, fructibus 3–6; pedicelli circ. 5 mm. longi; sepala florum valde defloratorum late vel satis anguste triangularia, partem liberam receptaculi aequantia, initio ut receptaculum lanuginosa, deinde ambo glabra; petala ignota; stamina ut videtur circ. 25; discus cupularis, glaber; styli 2, 2/3 connati, basi parce lanuginosi; ovarium totum inferum, carpellis ventre ut videtur tantum basi connatis in parte libera parce lanuginosis; fructus rubri, obovato-globosi, ad 12:12 vel 15:13 mm. magni, apice parte libera receptaculi et parte inferiore persistente stylorum coronati sepalis plus minusve deciduis, sparse punctati; semina obovalia, valde compressa, apice rotundata, basi sub hilo apiculata, 5–6 mm. longa, 3–3.5 mm. lata, flavo-brunnea.

Yunnan boreali-occidentalis: ad latera orientalia montium niveorum prope Lichiang-fu, alt. circ. 3200 m., Octobri 1914, *C. Schneider* (no. 3913, typus in Herb. Arb. Arn. et Hb. Schneider).

The nearest relatives of this species seem to be *S. Aria* Crtz. and *S. lanata* Koch, from both of which it may at once be distinguished by its much shorter sepals and the different serration and lobation of the leaves. The shape of

its rather narrow and long leaves is different from that of all the other Asiatic species of this group, and I cannot identify it with any species mentioned by REHDER in his *Conspectus specierum Asiae orientalis* (SARGENT, Pl. Wils. 2:272. 1915), nor with any other form known to me.

The name is given in honor of Count ISTVAN AMBROZY, a very successful garden maker on his famous estate at Malonya, Hungary, as a slight return for all his help in my dendrological studies.

SORBUS HUPEHENSIS Schn., var. **aperta,** n.var.—*S. aperta* Koehne in SARGENT, Pl. Wils. 1:465. 1913.—A typo praecipue recedit foliis (4–)5, non 6–8-jugis, foliolorum paribus in rhachide interstitiis plerisque 1.8–2.3 cm. longis separatis.

See my remarks under the following variety.

SORBUS HUPEHENSIS, var. **obtusa,** n. var.—A typo praecipue recedit foliis 4–5-jugis, foliolorum paribus in rhachide interstitiis 1.5–2.5 cm. longis separatis, foliolis apice distincte obtusis margine tantum triente superiori dentibus utrinsecus 3–9 serratis maximis lateralium ad 5.5:2.2 cm. magnis subtus sub microscopio undique satis dense papillosis.

Yunnan boreali-occidentalis: prope Yung-ning, 19 Junii 1914, *C. Schneider* (no. 1166; typus in Herb. Arb. Arn. et Hb. Schneider; arbor circ. 8 m. alta).

In determining the *Sorbus* of the *Aucuparia*-group collected by myself in southern Szechuan and northwestern Yunnan, I cannot refer the above form to any species or variety enumerated by KOEHNE in his *Sorborum chinensium conspectus analyticus* (SARGENT, Pl. Wils. 1:475. 1913). It seems to me most nearly related to *S. aperta* Koeh., from the type of which it differs by its 5–6 (instead of 4–5) pairs of leaflets which are distinctly obtuse at their apex and also distinctly papillose beneath. As in *S. aperta*, the pairs of leaflets are more distant on the rhachis, and the leaflets are somewhat larger than in typical *S. hupehensis*. Otherwise, var. *obtusa* seems to connect the latter with *S. aperta*, and I am unable to detect sufficient differences to keep *S. aperta* a distinct species. I make it, therefore, a variety of *S. hupehensis*, of which it represents the most northern form, chiefly distinguished by its fewer pairs of leaflets.

To the typical *S. hupehensis* Schn. (in Bull. Herb. Boiss. II. 6:316. 1906; and Ill. Handb. Laubh. 1:680, *fig. 374r, 775n.* 1906), I refer the following specimens of my own collections which, partly, may represent var. *laxiflora* (see later) if it is possible to keep this form even as a variety.

Szechuan australis: inter pagos Wo-lo-ho et Hun-ka, in silvis apertis montium, alt. circ. 3000–3400 m., 13 Junii 1914, *C. Schneider* (no. 3532; arbor circ. 10 m. alta, trunco circ. 0.6 m. crasso; flores odore valde ingrato).

Yunnan boreali-occidentalis: ad latera orientalia montium niveorum prope Lichiang-fu, in dumetis apertis, alt. circ. 3500 m., Octobri 1914, *C. Schneider* (no. 2829 et 3912; fructus maturi carnei); eodem loco et tempore (no. 2811; fructus carnei; gemmae apice distinctius rufo-lanatae); in angustiis montium inter Sung-queh et Teng-chuan, 29 Septembris 1914, *C. Schneider* (no. 2905; arbor ad 8 m. alta; fructus carnei; gemmae ut in no. 2811 rufo-lanatae; rhachis foliorum ad 9-jugorum apicem versus distinctius alata; folia surculorum a me in eadem arbore abscissorum minora ad 12-juga foliolis tantum ad 2:0.7 cm. magnis iis *S. Prattii* non absimilibus).

The fruiting branch of no. 2905 agrees well with that of no. 2811, both showing the buds distinctly fulvous at the apex, and the narrow wings of the rhachis. I do not know whether these two numbers represent another form because I have not yet seen fully developed buds of typical *S. hupehensis*.

In nos. 2829 and 3912 the buds are much more glabrous, and the rhachis is almost wingless. I am at a loss how to distinguish these specimens from the type of *S. laxiflora* Koehne collected by E. H. WILSON in western Szechuan, northeast of Tachien-lu, on the Ta-p'ao-shan, July 4, 1908 (no. 3008), and therefore I propose the following variety:

SORBUS HUPEHENSIS, var. **laxiflora,** n. var.—*S. laxiflora* Koeh. in SARGENT, Pl. Wils. 1:466. 1913.

It needs further investigation to determine how this variety may really be distinguished from typical *S. hupehensis*. KOEHNE himself says that *S. laxiflora* forms with *S. hupehensis* and *S. aperta* "a special group distinguished by its small stipules, medium-sized leaves with 4–7 pairs of medium-sized leaflets, and by a remarkably loose inflorescence."

There is another group of species described by KOEHNE which I cannot separate because the characters on which they are founded by the author are too variable according to my own observations. I therefore propose to unite them in the following manner:

SORBUS PRATTII Koeh., var. **tatsienensis,** n. var.—*S. munda* Koeh. in SARGENT, Pl. Wils. 1:469. 1913, includ. f.a. *tatsienensis* et f.b. *subarachnoidea*.—*S. pogonopetala* Koeh., l.c. 473.—A typo nonnisi foliolis paullo majoribus saepissime basi tantum integerrimis argutius et paullo profundius serratis differre videtur.

After a careful comparison of all the type numbers before me, I do not even know how to distinguish *S. munda* as a variety from *S. Prattii*. In describing *S. pogonopetala* the author apparently overlooked the fact that the type of this species (*E. H. Wilson's* no. 3003), a flowering specimen, and the only one the author has seen, came from the same locality (Pan-lan-shan, west of Kuan Hsien) as *Wilson's* no. 4323 which KOEHNE makes the type of his *S. munda* f. *subarachnoidea*. But this fruiting specimen agrees in every respect with the

flowering one, the only difference I can detect being that the pubescence is somewhat fulvous, while it is greyish in no. 3003. KOEHNE says: "*Sorbus pogonopetala* differs from all the other Chinese species with numerous small leaflets in its strongly bearded petals; it is also remarkable in the purplish black color of its petioles and rhachis." The last mentioned character is, in my opinion, judging by the co-type before me, of no value, and apparently only due to an effect of drying. The hairy petals are also present in *S. Prattii*, in the description of which the author himself says "petala . . . medio supra parce tenere lanato-barbata." I fail to see any difference between the "beards" of *S. Prattii* and of *S. pogonopetala*.

Of both *S. Prattii* and *S. munda*, KOEHNE has described two forms, the first one, of course, representing nothing else than the type. In reducing *S. munda* to a variety of *S. Prattii*, the name of KOEHNE's f.a. *tatsienensis* has to be used, according to international rules, as the new varietal name. It may also be mentioned that the presence or absence of papillae on the under surface of the leaves is a rather doubtful character to base any varieties or even species upon. In our case, the younger leaves of *S. pogonostyla* are "subtus epapillosa," while of *S. munda* they are described as "subtus sat valide papillosa, inter papillas parce v. haud reticulato-striata." In the specimen of *S. munda* (no. 4323) before me the leaves may better be described as "subtus satis indistincte papillosa," and the kind of papillae observed on the leaves of these species of *Sorbus* seems to be always much more indistinctly developed on the younger leaves than on the mature ones, and they are quite often entirely absent "non nisi circa stomata." After all, I believe we ought not to lay too much stress upon the development or absence of these papillae.

ARNOLD ARBORETUM
JAMAICA PLAIN, MASS.

PECULIAR EFFECTS OF BARIUM, STRONTIUM, AND CERIUM ON SPIROGYRA

S. S. CHIEN

(WITH TWO FIGURES)

It has been pointed out by OSTERHOUT[1] that dilute solutions of $BaCl_2$ (0.001–0.0001 M) have a specific effect on certain species of *Spirogyra*. They produce a peculiar contraction of the chloroplasts in the middle of the cell which is very characteristic. This effect was not produced at this dilution by any of the other salts examined. As specific effects of this kind are uncommon, it seemed desirable to investigate the matter further.

Two species of *Spirogyra* were investigated, a large form of the *S. crassa* type, which was used by OSTERHOUT, and a smaller species. The method of contraction differs somewhat in the two species. In both kinds contraction usually begins in the region near the ends of the cell, but in the larger kind the chloroplasts sometimes begin to contract in the central region. In a large percentage of the cells of the larger kind the central region shows the greatest contraction. The chloroplasts in this region may either shrink away from one side of the cell wall more than from the other, or equally from all sides. In the latter case the final shape (fig. 1, *B*) assumed by these bodies is quite typical for this kind of *Spirogyra*. In the smaller kind the greatest shrinking occurs in regions between the center and the ends of the cell (fig. 2, *B*). These are cells of the larger kind, however, whose chloroplasts contract like those of the smaller kind, and vice versa. In general the longer cells of each species are apt to contract most toward the ends, while the shorter cells are apt to have the greatest contraction in the middle. In either case the contractions of the chloroplasts are very characteristic.

Contraction usually takes place a few minutes after the application of the solutions. Table I shows the time necessary for producing the effect at different solutions.

[1] OSTERHOUT, W. J. V., Specific action of barium. Amer. Jour. Botany 3:481–482. 1916.

The last named dilution of each salt is the lowest dilution at which contraction appears. $CeCl_3$ produces contraction of the larger kind only. It is also seen from the table that the lower

TABLE I

For the larger kind of *Spirogyra*		For the smaller kind of *Spirogyra*	
Solution	Time in minutes	Solution	Time in minutes
$CeCl_3$ 0.005 M	8	$BaCl_2$ 0.05 M	1–2
0.001 M	9	0.01 M	2–5
0.0005 M	9	0.001 M	15
0.0001 M	9		
0.00005 M	10	$SrCl_2$ 0.05 M	2–3
		0.01 M	3–4
$BaCl_2$ 0.005 M	4		
0.001 M	5		
0.0005 M	7		
$SrCl_2$ 0.01 M	2.5		
0.005 M	12		

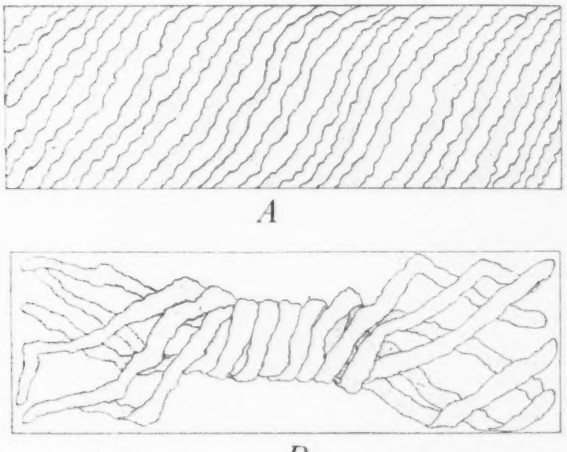
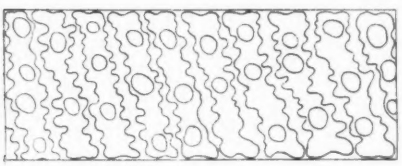


FIG. 1.—*Spirogyra*: *A*, normal condition; *B*, after treatment with $BaCl_2$

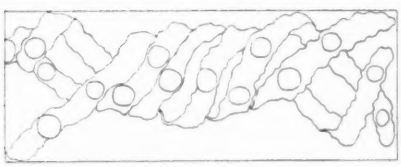
limit of $CeCl_3$ solution which produces the effect is less than that of the $BaCl_2$ solution, but the table shows that the effect is produced more rapidly in $BaCl_2$ and in $SrCl_2$ than in $CeCl_3$. These

two kinds of *Spirogyra* are different also in respect to the phenomena of antagonism, which will be discussed later.

If a contraction appears only after some hours or days, it is disregarded, as in such long experiments complicating factors are present. Solutions of barium and strontium salts in lower concentrations than those indicated will not produce the effect in 24 hours. With other salts which usually do not produce the effect contractions sometimes appear after 3 or 4 hours (or after several days), but this may be due to other agencies than the salts, because in material dying from natural causes cells with contracted chromatophores are sometimes found.



A



B

FIG. 2.—*Spirogyra:* large form, *crassa* type, pyrenoids omitted; *A*, normal condition; *B*, after treatment with $BaCl_2$.

The material used for this purpose must be fresh and in good condition, or it will lose its sensitiveness and fail to contract when the salts are applied. For example, material was taken at first from a glass jar kept in the greenhouse and was found to be sensitive to both barium and strontium. Later this material deteriorated because of the increased sunlight and heat of the greenhouse, and did not respond to $SrCl_2$, although still responding to $BaCl_2$. Still later it became insensitive to $BaCl_2$ solution, even at the concentration of 0.1 M. The same thing occurred with the small form which grew in a pond. This decrease of sensitiveness seems to be due to some chemical or physical change in the cell when its vitality is injured, which prevents the chromatophores from contracting.

As this visible effect of barium, strontium, and cerium is well suited to the study of antagonism, attempts were made to see what salts hinder or prevent these effects.

Some experiments were made with the smaller kind of *Spirogyra* in order to see whether antagonism occurs. $BaCl_2$ and $SrCl_2$ have no antagonistic action on each other. $CaCl_2$ and $CeCl_3$ (neither of which causes contraction of the chromatophores by itself) are able to antagonize $BaCl_2$, and $CeCl_3$ is more effective than $BaCl_2$. The chromatophores do not contract when placed in a mixture made by adding 10 cc. of 0.04 M $CeCl_3$ to 90 cc. of 0.08 M $BaCl_2$ in an hour and a half (after which the experiment was discontinued); while if 10 cc. distilled water is added to 90 cc. of the same $BaCl_2$, contraction begins after 1.5 minutes. Antagonism is obtained also by mixing 60 cc. of 0.1 M $Cacl_2$ with 40 cc. of 0.1 M $BaCl_2$. In this mixture no contraction occurs in 1 hour, while if 60 cc. of distilled water is used in the mixture in place of $CaCl_2$, the contraction occurs in 2 minutes. The proportions here mentioned are approximately the optimum ones for each mixture.

Summary

1. The chloroplasts of certain species of *Spirogyra* contract away from the cell wall in a peculiar and characteristic fashion in solutions $CeCl_3$, $BaCl_2$, and $SrCl_2$ (in the case of the smaller kind in the last 2 only). The effect is observed in dilutions as great as 0.00005 M $CeCl_3$ (in the case of the larger species), and in 0.0001 M $BaCl_2$. $SrCl_2$ also produces this effect, but not at such great dilutions as $CeCl_3$ and $BaCl_2$.

2. In the smaller species of *Spirogyra* the effect of $BaCl_2$ is inhibited when $BaCl_2$ is mixed with $CeCl_3$ or $CeCl_2$ in proper proportions.

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BRIEFER ARTICLES

MANIPULATING MICROSCOPIC ORGANISMS IN STAINING[1]

Perhaps the chief limiting factor in the successful preparation of permanent microscopic mounts of unicellular and colonial organisms is the difficulty of manipulation during the staining, with the incidental loss of the material in the necessary changing of the staining and washing solutions. The small size of such forms as *Sphaerella*, *Pandorina*, *Volvox*, *Pediastrum*, and the desmids renders these organisms especially liable to loss in these parts of the process. When handling the very small forms, the usual precautions taken in staining filamentous algae are generally wholly inadequate to prevent the loss of the material.

The difficulties in the way of success, however, may be overcome by using a funnel, filter paper, and a wash bottle, and combining the careful manipulations of quantitative chemistry, to prevent loss of valuable material, with the dehydration and staining methods of the Venetian turpentine method of mounting algae.[2] After the organisms have been killed in the usual 1:1:400 chromacetic acid solution, the entire contents of the vessel can be filtered, leaving the material to be stained on the filter paper in the funnel. Complete washing to remove the killing fluid can be secured by the use of the wash bottle. Should it be desirable to let the material stand in water for a few hours, the filter paper may be punctured and the material washed out into a beaker (this will save the work of washing). Refiltering later will leave the material on the filter paper and, with a little washing with water from the wash bottle, ready for the staining.

This manipulation is especially adapted to use with the iron-alum haematoxylin stain. The staining method itself may be greatly shortened, and in the modified form gives splendid results with these lower forms. The iron-alum should be dissolved in distilled water and all water treatments of material should be made with distilled water to avoid precipitates. Weak solutions of iron-alum should be used, 0.1 per cent solution at most. Frequently a few drops of a 1 per cent

[1] Contribution from the Department of Botany, Pennsylvania State College, no. 8.

[2] CHAMBERLAIN, CHAS. J., Methods in plant histology, 3d ed. Chicago, 1915.

solution in 100 cc. of water are sufficient. The iron-alum solution is applied slowly to the material on the filter paper in the funnel. After a short time, 15–30 minutes or even less being sufficient, the material is washed thoroughly with distilled water from the wash bottle. A weak haematoxylin stain is then applied slowly to the material, and repeated observations of specimen mounts under the microscope will determine when the staining is complete. A 0.1 per cent haematoxylin stain is strong enough, and 30 minutes or less time is long enough for it to act.

When the staining is complete, the differentiation of the stain is accomplished by a thorough washing in distilled water and the customary destaining with the 0.1 per cent iron-alum solutions. This latter step is the one requiring the greatest care, since it can be overdone most easily; the light haematoxylin stain used in the method is easily lost by prolonged treatment with even a very weak iron-alum solution. One application of the destaining solution is generally sufficient if care be taken that the material is thoroughly saturated with the solution. As usual when using the iron-alum solution for differentiating a stain, the process should be closely observed under the microscope. It is to be understood that no directions concerning the time limits can be given for the use of either the staining or differentiating solutions, since success depends upon the proper balancing of these two processes. When the stain has been properly differentiated, the material should be thoroughly washed with distilled water from the wash bottle. At any stage of the process, should it be desired to allow the material to remain covered by the solution being used, this can be accomplished by fitting a short piece of rubber tubing over the stem of the funnel and using a clamp to stop the flow of the solution.

Dehydration is accomplished by the glycerine dehydration method in general use. The transfer to the 5 per cent glycerine solution is made by puncturing the filter paper and washing with the glycerine solution into an open vessel, such as a Petri dish. The minimum amount of glycerine should be used, since it is difficult to remove. After a few days' exposure to evaporation, the glycerine solution is concentrated. The material is again poured into the filter paper in the funnel and complete dehydration accomplished by washing all the glycerine out with 95 per cent alcohol, followed by absolute alcohol to complete dehydration. There should be no doubt about the thoroughness of this part of the process, since complete dehydration is essential to success. When completely dehydrated the material is transferred quickly to a 10 per cent Venetian turpentine solution and placed in a

desiccator and allowed to concentrate according to the directions given for the Venetian turpentine method.

Should it be desired to use some of the other stains, such as the Magdala red-anilin blue combination recommended for algae, it will be necessary to modify this manipulation to suit the method. Since these stains are used in strong alcoholic solutions, the material to be stained is washed after killing by the method already described, and then dehydrated by the glycerine method before staining. The glycerine is washed out with 95 per cent alcohol and the stains applied.

Summary

1. Treat the material the proper length of time in a suitable killing solution.
2. Filter the material to remove killing solution, leaving the material on the filter paper in the funnel.
3. Wash with distilled water from a wash bottle.
4. Treat with a 0.1 per cent (or less) iron-alum solution.
5. Wash with distilled water, using wash bottle.
6. Stain by application of 0.1 per cent (or less) aqueous haematoxylin stain.
7. Wash with distilled water.
8. Differentiate the stain with 0.1 per cent iron-alum solution, washing with distilled water very thoroughly after the treatment.
9. Dehydrate with glycerine and mount by Venetian turpentine method.
10. Vary the treatment, when alcoholic stains are to be used, by dehydrating before staining.—J. BEN HILL, *Pennsylvania State College, State College, Pa.*

THE BOTANICAL STATION AT CINCHONA

The Botanical Station at Cinchona, in the Blue Mountains of Jamaica, which from 1903 to 1913 was leased by the New York Botanical Garden, has now been leased by the Smithsonian Institution, on behalf of 14 American botanists and botanical institutions that have contributed the rental. These botanists and institutions believe that there is need in the American tropics for a counterpart of the famous Buitenzorg Garden of Java. They hope that the opening of this laboratory at Cinchona may prove as stimulating to the development of botany in

this country as the opportunities afforded at Buitenzorg have been to the advance of this science in Europe.

The equipment available at the Station consists of the residence with its furnishings, 3 laboratory buildings, 2 glass propagating houses, and a garden of 10 acres containing many species of exotic shrubs and trees, besides many native plants from the highlands of Jamaica. The occupant of Cinchona is also free, within reasonable bounds, to study and collect plants over the many thousand acres of the whole Cinchona reservation, as well as in the neighboring valleys belonging to private owners. He will likewise be given every available facility for study at Hope Gardens, where he will find an herbarium, a library, and an extensive collection of tropical plants. The same privilege will be his at Castleton Garden, which contains fine collections of cycads and palms, and of *Ficus* and other dicotyledonous trees.

The many different types of native vegetation accessible from Cinchona and from Hope include a number of great ecological interest and numerous species of importance for the morphologist, cytologist, and physiologist. The ecological types range from the cool mountain forest with its tree ferns, epiphytes, and water soaked filmy ferns, to the hot, steaming woods of the lowlands of the north side at one extreme, and to the dry savannas and cactus deserts near Kingston at the other. Fuller statements of the opportunities for research in various lines, written by men who have worked there, may be found in *Science* **43**:917. 1916 (see also *Popular Science Monthly*, January 1915).

Any American investigator may be granted the use of the Cinchona Station by the Cinchona Committee, which consists of N. L. Britton, John M. Coulter, and Duncan S. Johnson. Applications for this privilege and for information regarding the conditions under which it is granted should be sent to the writer.—Duncan S. Johnson, *Johns Hopkins University, Baltimore, Md.*

CURRENT LITERATURE

BOOK REVIEWS

Vegetation of Paraguay

CHODAT[1] has issued the first of a series of bulletins upon the plants of Paraguay. The work on which the series is based includes investigation continued at intervals since 1889 and culminating in an expedition made in 1914 by CHODAT and his former pupil VISCHER, and authorized by the Federal Department of the Interior of Switzerland. Sketches, water colors, and photographs were made in the field, as were also some chemical tests. A large quantity of material was brought home for later study.

The first chapter treats of the climatology and physiography of the country. The discussion of climate is based upon records covering 30 years, made by BERTONI at Asuncion on the Paraguay River and at Puerto-Bertoni on the Alto-Parana. The eastern part of Paraguay has a subtropical climate of the Chinese type; the western part is more like the Mediterranean region. Topographically, the state may be divided into the depressions along the Paraguay River and the mountains of the east. A lower highland of about 300 m. elevation separates the 2 main depressions, that about Lake Ypacarai and the lowland around the Ypoa lagoon. This cordillera extends nearly east and west between the Rio Salado and Rio Manduvira, and these 2 depressions are the regions under discussion in this paper.

CHODAT then takes up the Solanaceae, a group of intermediate importance, which compose several distinct formations, and gives somewhat in detail the variations in adaptation for climbing found in the liana forms, and the anatomical changes which occur during curvature. Only a few species are insect pollinated, those having large tubular flowers being visited by lepidopterous insects and humming birds. The genera *Sessea* and *Grabowskia* are here reported for the first time for the Paraguay flora. Indigo was found present in 2 species not previously known to contain the pigment. A few species of the family find in Paraguay their southern limit, while a somewhat larger number reach here their most northern extension. Several are mentioned as endemic and some of these are extremely local. In the third chapter the author discusses the Hydnoraceae, largely from a morphological standpoint. The one genus given (*Prosopanche*) is reported as parasitic on the roots of *Prosopis* and some of the Solanaceae.

[1] CHODAT, R., and VISCHER, W., La vegetation du Paraguay. 1st fascicle. 8vo. pp. 157. *pls.* 3. *figs.* 123. Genève. 1916.

The last chapter deals with the dominant group of the region, the Bromeliaceae. The 2 main divisions considered are the cistern plants and the epiphytic *Tillandsias*. The latter are divided into those which lean against the support and those having some means of attachment to it. The different adaptations for climbing are illustrated. The structure and function of the hairs of *Tillandsia* and of the hairs on the submerged leaf bases of the cistern species are given particular attention. The presence of cortical roots in the attached lianas is also noted and their value to the plant discussed. Here, as in the Solanaceae, insect pollination is not very common, but the humming bird is a regular visitor to some large-flowered species. A few of the Bromeliaceae, as *Tillandsia usneoides* and *T. recurvata*, have a range from southern United States or Mexico to the southern part of South America. Most of the species mentioned, however, are limited to South America, 9 being given as endemic. The author also includes in this chapter a very interesting description of the xerophytic rupicole species belonging to various families which are found on the rocks of Cerro San Tomas and Sierra d'Acahay.—ARAVILLA TAYLOR.

NOTES FOR STUDENTS

Puget Sound algae.—A fascicle of papers[2] from the Puget Sound Marine Station at Friday Harbor, Washington, gives the results of work done on algae at the station, largely during the summer of 1916.

Miss HURD finds that young bladder kelps (*Nereocystis*) can adapt themselves to 55 per cent of fresh water in their environment if the change is made gradually. She concludes that rapid elongation of this plant is due to low light intensity in the water, and that growth of the stipe is greatly retarded by strong light when the bulb approaches the surface of the water. The fact that this does not act as a very exact determiner of length is readily understood, when we remember that the variation from extreme high tide to extreme low tide during the growing season in this region is more than 12 ft. She reaches the conclusion that there is no relation between rate of growth and mechanical stretching in the stipe of the plant. The experimental evidence given seems to justify this conclusion, providing that nothing else (for example, light) was a limiting factor in both experiment and control.

In another paper Miss HURD decides that the *Codium adhaerens* (Cabr.) Agardh reported from San Juan Islands and probably that from all of Puget Sound is *C. dimorphum* Sved., since it has no utricle hairs and has two types of utricles, the one with unmodified end wall and the other with thickened, striated end wall. She believes that the variation in the predominance of thick or of thin end walls in the utricles is probably due to differences in environment. The thick-walled type sometimes predominates over the whole

[2] Puget Sound Marine Station Publications 1:nos. 17–24. 185–248. *pls. 33–466*. 1916.

thallus, sometimes is found only around the margin and on the under side of the lobes, and sometimes is wanting entirely.

MUENSCHER reports a list of marine algae found on Shaw Island (one of the San Juan group), with notes as to zonal distribution and relative abundance, and a discussion of the ecological factors involved. He finds 54 Rhodophyceae, 31 Phaeophyceae, 15 Chlorophyceae, and 3 Myxophyceae. The plates give the distribution at various points on the island and will be very useful to collectors of algae in the region.

Miss KIBBE reports the presence of a parasitic fungus (*Chytridium alarium*, sp. nov.) on *Alaria fistulosa* collected in Alaska. She examined all of the species of brown algae that were readily available at the Puget Sound Marine Station, and also specimens of *Alaria valida* from Alaska, and did not find any trace of this fungus in any of them. In *A. fistulosa* she found the fungus in various forms in all parts of the plant except the heavy older portions of the stipe.

Miss KARRER finds that some light is thrown on the metabolism of *Nereocystis* by chemical reactions whose results are seen under the microscope. She finds that the cell walls are made up of cellulose and algin, the latter being probably the substance that holds the cells together. She finds that the presence of the inorganic substances (calcium, magnesium, sodium, potassium, chlorine, sulphates, carbonates, phosphates, and iodine) whose presence in the plant have often been shown by analytical chemists can be demonstrated in the cell by using the methods suggested by TUNMANN[3] and MOLISCH[4] with slight modifications.

Miss CLARK reports the acidity of marine algae as determined by titration. She reports that all of the 31 species tested were acid.

LANGDON[5] finds that carbon monoxide is present in the float of the bladder kelp (*Nereocystis*), the quantity varying considerably in different individuals. He finds the presence of carbon dioxide to be only occasional and the quantity minute. He does not find confirmation of previous work tending to show that the quantity of carbon dioxide and of oxygen vary with the time of day. He suggests that since theories of photosynthesis have largely been concerned with carbon monoxide and its reduction product formaldehyde, and with formic acid, of which carbon monoxide may be considered the anhydride, it is possible that the occurrence of carbon monoxide in plant tissues may be more general than has been supposed. Apparently LANGDON'S work is the first demonstration of free carbon monoxide in a living plant. A large plant cavity surrounded by rapidly growing tissue furnishes an unusually favorable opportunity for the investigation of gases taking part in metabolism. The sieve tubes in this plant are in the mycelium-like pith web on the interior surface of

[3] TUNMANN, O., Pflanzenmicrochemie. Berlin. 1913.

[4] MOLISCH, H., Microchemie der Pflanzen. Jena. 1913.

[5] The substance of this paper has also been published in Jour. Amer. Chem. Soc. **39**:149–156. 1917.

the float. Since the whole surface of the sieve tubes in this portion of the plant is thus exposed to the gas contained in this float, it would seem possible that considerable oxidation of foods is carried on in this internal atmosphere. The gas in this float is shown to contain a little larger percentage of oxygen than air. It may possibly be worth while to consider the presence of carbon monoxide in plants in connection with the wide distribution of oxidases in plant tissue and the possible mechanism of their reaction.[6] LANGDON'S thorough demonstration of the presence of carbon monoxide in this cavity is a very important piece of work, and great interest attaches to the possible relation of this gas to the metabolism of the plant.—G. B. RIGG.

Quantitative characters in beans.—By means of a statistical study of pole and bush beans, EMERSON[7] has analyzed the characters causing height variation in *Phaseolus vulgaris*. They are 3 in number and apparently segregate independently after crossing. First is the manner of growth, which is either "determinate" (bush type) or "indeterminate" (pole type), with the indeterminate habit completely dominant in the F_1 generation, and showing the typical 3:1 splitting in the F_2 generation. Such behavior he interprets as the result of a single pair of freely segregating factors behaving in a Mendelian fashion.

TSCHERMAK, using the hybrids *Phaseolus vulgaris*×*P. multiflorus* and the reciprocal, found anomalous splitting in the F_2, since some of the "short" segregates produced "talls" in succeeding generations. He makes no mention of habit of growth, and merely classifies the progenies as "talls" and "shorts." The results of TSCHERMAK need not be compared with EMERSON'S, however, because in the former case the hybrids are interspecific, and in the latter intervarietal (intraspecific).

The second character operative in determining height is number of internodes. The presence of this character was deduced from the fact that different varieties of both pole and bush beans differed in the number of internodes produced when grown under the same conditions. The question then arose as to whether this tendency to produce few or many internodes could be inherited independently of habit of growth. Suitable crosses were made and the results seemed to answer the question in the affirmative, although the evidence is admittedly incomplete. The factors determining this difference could not be shown to be perfectly dominant, but apparent segregation followed hybridization. This segregation was attended in the F_2 generation by a range of variability exceeding that of the 2 parents. EMERSON interprets this result as due to the action of multiple segregating factors.

The third character involved in height is length of internode. The modification of this character by habit of growth made its behavior difficult to study.

[6] REED, G. B., BOT. GAZ. **62**:53–64. 1916.

[7] EMERSON, R. A., A genetic study of plant height in *Phaseolus vulgaris*. Research Bull. no. 7. Nebr. Agric. Exp. Sta. pp. 73. 1916.

In order to have a standard of comparison between pole and bush bean types, the first 5 internodes were measured and the means computed. For comparison between different varieties of pole beans the mean of the first 5 internodes was used. It was thought that the actual internode length found for some of the bush varieties might not be representative of the potential length which would have been attained by the upper internodes had not the production of a terminal inflorescence hindered further growth. To test this supposition crosses were made between a bush bean with long internodes and a pole bean with short internodes. The resulting hybrid showed an intermediate development in the F_1 and a wide range of variation in the F_2 generation. Bush beans with shorter internodes and pole beans with longer internodes than the parent types exhibited were obtained. Here again the variations were attributed to the action of multiple, non-dominant, independently segregating factors.

In conclusion, the author points out that the results of other investigators tend to show that quantitative characters in plants are inherited in two ways: (*a*) they are due to the action of a single Mendelian pair of factors showing complete dominance in the F_1 and a 3:1 ratio in the F_2 generation; (*b*) they exhibit an intermediate development in the F_1 and a wide range of variation in the F_2 generation. In class (*a*) belongs the determinate as opposed to the indeterminate habit of growth. Characters such as length and number of internodes fall into class (*b*). Such characters as those of class (*b*) have been interpreted in 2 ways. EMERSON, TSCHERMAK, EAST, and others attribute them to the interaction of many independently segregating factors, a theory in accord with the multiple factor hypothesis of NILSSON-EHLE. CASTLE, however, has interpreted such behavior as due, in some cases, to the modification of a unit factor through hybridization. In the case of the bean crosses, EMERSON implies that the factor involved would be that which determines habit of growth. After discussing this latter hypothesis and the assumptions its adoption would necessitate, he rejects it in favor of the multiple factor hypothesis.

Since, therefore, the characters involved in producing an effect seem to behave in different manners in inheritance, the author explains the variation in height following hybridization between pole and bush beans as due to the modification of the expression of a unit factor by the presence or absence of a number of factors producing other effects (as, for example, the effect of the determinate habit of growth on the potential length of internodes and on the number of internodes, etc.). However, the author disavows any intention of maintaining that this is the only possible explanation, and suggests that it may have to be modified to suit the results of further selection and hybridization experiments.—WILBUR BROTHERTON.

Philippine forests.—Our knowledge of the economic importance and the environmental conditions of some tropical forests has been advanced by a

recent publication,[8] the joint product of a botanist and a forester. The former seems to have contributed many details concerning the floristic and ecological composition of the many variations in the dipterocarp forest. The quantitative data regarding the physical climatic factors are among the first to be collected in tropical forests according to modern methods. Soil moisture determinations for every month in the year, although unfortunately not accompanied by the wilting coefficient of the soil, show that the soil is quite uniformly moist throughout the year. Atmometer records throughout the year give for the first time the data for an adequate comparison with the evaporating power of the air in mesophytic forests elsewhere. In the dipterocarp forests of Mount Maquiling the maximum, minimum, and average daily rates of evaporation upon the floor of the forest are respectively 5.3, 0.7, and 2.5 cc., as compared with 10.6, 3.3, and 7.1 cc. obtained by the reviewer[9] in the mesophytic beech-maple forest of northern Indiana. The evaporation data are especially good because they are given not only for the floor of the forest but also for the second story trees, where there is protection by the general canopy of foliage, and give a maximum, minimum, and average daily rate of 7.5, 1.8, and 5.3 cc. respectively, and for the atmosphere above the tree tops, where the maximum, minimum, and average daily rates are 22.1, 8.4, and 15.7 cc. The leaves of the tree tops are thus exposed to an evaporating power of the air 6 times as great as that obtaining for the ground vegetation.

The forester's part of the report contains many data of the distribution, composition, volume, and rate of increment of these forests. The results show that they may, when cut and logged by modern methods, make a very important contribution to the lumber supply of the world. In this connection it is interesting to note that the average rates of growth of the dipterocarps are about the same as those of the hardwoods in the central deciduous forest region of the United States; while one of the most rapid growers, *Parashorea plicata*, appears to grow about twice as fast as *Liriodendron*. The relative advantages of various cutting systems are discussed, and the opinion expressed that planting of dipterocarps is not likely to be successful.

This article, together with the earlier reports of WHITFORD, gives a good general ecological knowledge of these interesting forests, and should furnish a good basis for the rapid evolution of methods of forestry which will render these natural resources a permanent source of wealth for these islands.—GEO. D. FULLER.

Distribution of species.—WILLIS in two recent papers[10] attempted to show that the geographical distribution of species within Ceylon is to be explained, not by natural selection, but by the relative local age of each species, basing his

[8] BROWN, W. H., and MATHEWS, D. M., Philippine dipterocarp forests. Phil. Jour. Sci. Sect. A. **9**:413–561. *figs. 16.* 1914.

[9] BOT. GAZ. **58**:193–234. 1914.

[10] Rev. in BOT. GAZ. **61**:82. 1916; **62**:100. 1916.

argument upon statistics. In accordance with his theory he made a number of predictions as to the distribution of species in New Zealand. These predictions have been verified by statistics which he has collected there, and which he presents in his latest paper, furnishing a very striking verification of his theory.[11]

Supposing a given species to have entered the islands at a certain point, and spread at an even rate, the area of its distribution at any time would be a measure of its local age. It is reasonable to suppose that this species would give rise to endemics, in increasing number as time went on, and as the area occupied became greater. At the limits of the islands farthest from the point where the species entered, the local age of the species, and consequently the number of endemics to which it had given rise, would be least. Following out such a conception, WILLIS predicted that the middle zones of the islands should show a greater number of endemics than the outer zones, and this proved to be the case.

Following the same line of thought, those endemics which were produced early would have most nearly reached the limits of the islands in their distribution, while those produced later in the local history of the parent species would be more limited in their distribution to the middle zones of the islands. Consequently, the author predicted that "the range of an endemic species would on the average be greater the nearer that one of its limits was to either end of the islands." This also was verified.

Another prediction made and verified was that widely distributed species would be more widespread within the islands than endemics, as in the case of Ceylon. On the basis that the land connection with New Zealand both ended earlier and began earlier than that with Ceylon, the author predicted that the average area occupied by a species in New Zealand would be greater than in Ceylon, that is, that both "wides" and endemics would be comparatively fewer in the lower or earlier stages in the scale. These predictions also were verified.

Those who wish to examine the exact mathematical statement of the author's method and conclusions are referred to the paper.—MERLE C. COULTER.

A floating reed swamp.—Occurring in the delta of the Danube River is a remarkable form of floating swamp formed by the reed *Phragmites communis* var. *flavescens* Gren. and Godr. It has been described by Miss PALLIS,[12] who visited and studied it in 1912 and again in 1913. She found that this swamp, known as Plav, differs from a closed reed swamp chiefly in the fact that it floats, the surface of the mat of soil and vegetation remaining constantly about

[11] WILLIS, J. C., The distribution of species in New Zealand. Ann. Botany **30**: 4–457. *fig. 1.* 1916.

[12] PALLIS, MARIETTA, The structure and history of Plav, the floating fen of the delta of the Danube. Jour. Linn. Soc. **43**: 233–290. *pls. 11–25.* 1916.

4 cm. above the fluctuating surface of the water. These fluctuations of the water level are great, as there are usually 3 floods each year, 2 in spring and 1 in autumn, the water at such times rising 1–6 m. The floating mat is made up almost entirely of vertical rhizomes of the reed, which, with the aid of their roots, retain much soil, the whole attaining a thickness of 0.8–2 m. The aerial shoots vary in height from 1.2 m. to 5.15 m. This mat originates attached to the soil, but becomes floating with the death of the basal rhizomes and the action of such floods as are accompanied by only small depositions of silt. The maximum size of units becoming detached is given as 2500 sq. m. In the shallower water much of the reed mat remains permanently attached. Little other vegetation is mingled with the *Phragmites*, its only competitor being *Typha angustifolia*, which is apparently only able to inhibit its growth for a short time. The reed seems to be succeeded by *Cladium mariscus* or by an aggregation of species of *Carex*.

The most remarkable part of this paper is the hypothesis offered to explain the difference in size of the reed, varying as it does from 1.2 m. to 5.15 m. This Miss PALLIS ascribes, not to any difference of variety, but to a difference in age. She believes that the giant shoots, 5 m. in height, have arisen earliest and at the base of the branch system of the rhizoids, and that with progressive advancement toward the higher parts of the branch system the aerial shoots have become gradually smaller and shorter. The change in size is thus a senile degeneration which ultimately results in the death of the individual. Unfortunately, the necessary experimentation to prove this theory would extend over many years and hence could not be undertaken. Many of the facts appear to support Miss PALLIS' hypothesis, and most of her argument seems sound, but some of the evidence seems to point to overcrowding being at least one factor in the reduction in size of shoots. More data regarding the germination and early growth of the reed should shed light upon the question of the duration of life of the *Phragmites* and its final senescence and death.—GEO. D. FULLER.

Taxonomic notes.—DUCKE,[13] in a presentation of new and little known plants of the Amazon region, discusses 146 species, 102 of which are Leguminosae. There are 34 new species described, 21 of which are Leguminosae. Among the new species there is a *Zamia* (*Z. Lecointei*). The paper appears in the initial number of a journal issued by the Botanical Garden of Rio de Janeiro.

GREENMAN[14] has published the second part of his monograph of *Senecio*, including the AUREI (§ 6). He recognizes 48 species and describes 5 of them as new. Of the new species, 2 are from the region of Newfoundland and

[13] DUCKE, A., Plantes nouvelles on peu connues de la région amazonienne. Archiv. Jard. Bot. Rio de Janeiro **1**:1–150. *pls. 19*. 1915.

[14] GREENMAN, J. M., Monograph of the North and Central American species of the genus *Senecio*. Part II. Ann. Mo. Bot. Gard. **3**:85–194. 1916.

northern Maine, 2 from Utah and Nevada, and 1 from Mexico. In addition to the full descriptions and synonymy, the citations of stations and exsiccatae are very complete.

GRIFFITHS[15] has described 9 new species of *Opuntia*, which have been growing under his observation for 5–8 years.

PITTIER[16] has published a revision of *Inga*, a large American genus of leguminous trees, which has not been revised since 1875. He recognizes 212 species, 40 of which are new, representing 5 sections, which are further subdivided into series.

RENDLE[17] has published *Maidenia* as a new genus of Hydrocharidaceae from West Australia. It is a delicate water plant 5–6 cm. high, covered with numerous threadlike leaves, and belongs to the Vallisnerieae.

WERNHAM,[18] in a seventh paper on the Rubiaceae of the American tropics, has published an analytical key to the genera. The extensive display of Rubiaceae in this region is indicated by the fact that 182 genera are recognized, distributed among 21 tribes.

WRIGHT[19] has published a new genus (*Thuranthos*) of Liliaceae from South Africa, related to *Drimia* Jacq.—J. M. C.

Excretion of acids by roots.—HAAS[20] has taken up the much controverted question, do roots give off acids other than carbonic? He grew roots of early sweet corn in distilled water for 5 and for 19 days and tested the H+ concentration of the water against standard buffer solutions of phosphates with phenolphthalein as the indicator. He concludes that no acid other than carbonic is excreted by roots, but that decay of the roots does give a slight increase in the alkalinity of the water. The author says "The problem is important not only because acids dissolve plant food from the soil, but also because it involves the fundamental questions of the reaction of protoplasm and of the mechanism of excretion." This is true, but to answer the question in a way applicable to natural conditions one should not put them in the abnormal conditions offered by distilled water.[21] One might also expect the

[15] GRIFFITHS, DAVID, Additional species of *Opuntia*. Bull. Torr. Bot. Club **43**: 523–531. *pl. 30*. 1916.

[16] PITTIER, HENRY, Preliminary revision of the genus *Inga*. Contrib. U.S. Nat. Herb. **18**:173–223. *pls. 81–105*. 1916.

[17] RENDLE, A.B., A new genus of Hydrocharidaceae. Jour. Botany **54**:313–316. *pl. 545*. 1916.

[18] WERNHAM, H. F., Tropical American Rubiaceae. VII. Jour. Botany **54**: 322–334. 1916.

[19] WRIGHT, C. H., Diagnoses Africanae. LXIX. Kew Bull. 1916:no. 9. p. 233.

[20] HAAS, A. R., The excretion of acids by roots. Proc. Nat. Acad. Sci. **2**:561–566. 1916.

[21] TRUE, R. H., The harmful action of distilled water. Amer. Jour. Bot. **1**:255–273. *fig. 1*. 1914.

author to relate his work to the rather extensive work done on the differential absorption of ions by plant structures and the resulting changes in the reaction of the substratum.[22] This promises explanation of the corrosive action of roots, their great power to absorb salts from soils, as well as their ability to redden neutral litmus. On account of this process some method other than that used by the author will probably need to be employed for investigating acid secretion in natural growth conditions, in the presence of nutrient solutions or soil. The value of this work as a basis for a general conclusion is doubtful, considering that only two experiments were performed on a single species, and these in an abnormal condition.—WM. CROCKER.

Subantarctic and New Zealand floras.—SKOTTSBERG[23] has continued the series of comparisons made between the floras of portions of the southern hemisphere characterizing the previous work of HOOKER, DIELS, SCHIMPER, WERTH, CHEESEMAN, and CHILTON, and revising the list of bicentric types by taking recent additions to the flora of Subantarctic America and New Zealand into consideration. The list includes 49 orders. These may be referred to groups comprising (1) an Australian and New Zealand element in America, (2) an Andine element in New Zealand and Australia, and (3) an old Antarctic element which is more strictly bicentric. Of the last group *Nothofagus* is a striking example, with 6 species in New Zealand, 1 in Tasmania, 1 in Tasmania and New South Wales, 1 in New South Wales, and 8 in Chili with 3 extending to Fuegia.

He includes some recent evidence from fossil plants found in Graham Land, and concludes that there existed an Antarctic Tertiary flora resembling the present floras of Subantarctic America, New Zealand, and Australia, and that the Antarctic continent may have been a center of evolution from which plants and animals wandered north. The present flora is due therefore to a combination of old wanderings, the extinction of certain species during the Ice Age, the survival of others, and finally transoceanic migrations, which, if they ever took place, are still going on.—GEO. D. FULLER.

Subalpine plants of the Rocky Mountains.—Adding to a series of phytogeographical papers upon the Rocky Mountain region already noted,[24] RYDBERG[25] has analyzed the subalpine flora of the region. It consists of about 800 species, of which only 10 per cent are entirely restricted to the subalpine zone. About 20 per cent of the whole number are transcontinental plants,

[22] SKENE, M., The acidity of *Sphagnum* and its relation to chalk and mineral salts. Ann. Botany **29**:65–87. 1915.

[23] SKOTTSBERG, CARL, Notes on the relations between the floras of Subantarctic America and New Zealand. Plant World **18**:129–142. 1915.

[24] BOT. GAZ. **62**:83–84. 1916.

[25] RYDBERG, P. A., Phytogeographical notes on the Rocky Mountain region. **VI.** Distribution of the subalpine plants. Bull. Torr. Bot. Club **43**:343–364. 1916

while another 20 per cent are found also in the Pacific mountains, leaving 60 per cent peculiar to the Rockies. Of these, fully one-half are restricted to the southern Rockies, and less than one-fourth to the northern Rockies. Of the locally endemic species, which are all herbaceous, 6 are confined to the Canadian Rockies, 3 to Montana, 3 to Idaho, 14 to Wyoming, 13 to Utah, and 16 to Colorado. *Viola biflora* is noted as having the most remarkable distribution, having been found only in a few places in Colorado, in Alaska, and in Europe.—GEO. D. FULLER.

A polycotyledonous bean.—HARRIS[26] has secured a race of the common garden bean which shows steadily more than 2 cotyledons as tested by 3 offspring generations, comprising thousands of individuals. Since the race appears in a "pure line" and has remained constant in several differential features, he concludes that its origin and behavior are characteristic of mutation as defined by DEVRIES. The cotyledons are highly variable in number, ranging from 2 to 7, but have a modal frequency of 4. For this reason the embryo is described as tetracotyledonous. This persistent tendency of a dicotyledonous type to develop polycotyledony is an interesting confirmation of the claim that the number of cotyledons developed depends upon conditions rather than upon inevitable inheritance.—J. M. C.

Illinois Academy.—The volume of *Transactions* of the Illinois Academy of Science for 1915 has just appeared. It contains the following botanical papers: Comparison of a Rocky Mountain grassland with the prairie of Illinois, by GEORGE D. FULLER; Studies in *Phyllosticta* and *Cercospera*, by ESTHER YOUNG; Method of prophesying the life duration of seed, by JAMES E. GROVES; Peculiar examples of plant distribution, by H. S. PEPOON; The grass flora of Illinois, by EDNA MOSHER; A Florida smut, *Ustilago sieglingiae*, in Illinois, by MARGARET MEHLHOP. A symposium on colloids includes the following papers: Outline of the chemistry of colloids, by D. A. MACINNES; Significance of colloidal chemistry in physiology, by WILLIAM CROCKER.—J. M. C.

Bog theories.—The vegetation of peat bogs exhibits such remarkable peculiarities of habit and structure that it has called forth a number of varied and somewhat conflicting explanatory theories. These theories have been summarized carefully by RIGG,[27] especially in so far as the xerophily of the plants is concerned, in a manner that is likely to prove very useful. A good bibliography adds to the value of the paper.—GEO. D. FULLER.

[26] HARRIS, J. ARTHUR, A tetracotyledonous race of *Phaseolus vulgaris*. Mem. N.Y. Bot. Gard. **6**:229–244. 1916.

[27] RIGG, G. B., A summary of bog theories. Plant World **19**:310–325. 1916.